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FOREST RAY MOULTON, Editor

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FOREWORD

It is the policy of the American Association for the Advancement of Science to publish symposia presented at its meetings that "are on subjects of such importance and are of such quality that it can not afford not to publish them." The symposia heretofore published by the Association because they were deemed to measure up to these standards have been *The Cancer Problem* (1937), *Tuberculosis and Leprosy* (1938), *Applications of Surface Chemistry in Biology* (1938), *Recent Advances in Chemical Physics* (1938), *Syphilis* (1938), and *Mental Health* (1939).

This symposium on *Problems of Lake Biology* was organized by the Limnological Society of America, an affiliated society of the Association. In providing facilities for presenting the symposium and in publishing and distributing it, the Association assists one of its affiliated societies in advancing the interests of a relatively new field of science. The great value of a systematic, comprehensive and documented survey of a rapidly developing science is obvious, for it establishes a solid foundation for future work and presents an outline of a region largely to be explored. This symposium, which was planned by a committee of distinguished specialists in the field, has these qualities.

Perhaps no other biological subject involves a greater variety of interrelated factors than lake biology. On the one hand, there are such physical factors as the size, shape and depth of the lake, the source and temperature of its water, its drainage, the winds that ruffle its surface, the hydrostatic pressures at various depths, and all the complexities of the light of different wave lengths it receives at various depths during the daily and seasonal cycles. The chemical factors are no less numerous and im-

portant, among which are the water content of diffused oxygen, carbon dioxide, nitrogen and hydrogen ionizations, and the amounts in solution of compounds of calcium, iron, silicon, phosphorus and other elements. In addition, there are numerous ever-changing and interacting organic compounds.

Finally, there is the cooperating and competing life itself, both plant and animal, both microscopic and macroscopic. In some cases the cooperation is direct—organism with organism or classes of organisms with other classes; the same is true of competition. In other cases the cooperation or competition is indirect—certain organisms or classes of organisms affecting the environment, physical, chemical or biological, to the advantage or disadvantage of other organisms or classes of organisms. In the light of the discussions in this volume, lakes themselves may be regarded in a sense as organisms having innumerable interesting characteristics and entrancing life histories.

Anyone not familiar with lake biology will be impressed with the great variety and abundance of life in lakes and in the sands along their shores. For example, at a distance of 150 centimeters from the shores of certain lakes which were studied there were, on the average, in ten cubic centimeters of sand 4,000,000 bacteria, 8,000 Protozoa, 400 Rotatoria, 40 Copepoda, and 20 Tardigrada. In a lake of moderate dimensions there are probably more individual living organisms than there are vertebrate animals on the whole earth. Naturally this abundant and interesting life in a complex, varied, ever-varying, and easily accessible environment offers rare opportunities for investigating fundamental problems of the organic world.

F. R. MOULTON



LIST OF CONTRIBUTORS

GEORGE L. CLARKE, PH.D.

Instructor and Tutor, Department of Biology,
Harvard University, Cambridge, Mass.;
Junior Biologist, Woods Hole Oceanographic Institution, Woods
Hole, Mass.

FRANK E. EGGLETON, PH.D.

Associate Professor of Zoology, University of
Michigan, Ann Arbor, Mich.

F. E. J. FRY, PH.D.

Ontario Fisheries Research Laboratory, Department of
Biology, University of Toronto,
Toronto, Ont., Canada

ARTHUR T. HENRICI, M.D.

Professor of Bacteriology and Immunology, University of
Minnesota, Minneapolis, Minn.

ROBERT W. PENNAK, PH.D.

Instructor in Zoology, University of Colorado,
Boulder, Colo.

G. W. PRESCOTT, PH.D.

Associate Professor of Biology, Albion College,
Albion, Mich.

D. S. RAWSON, PH.D.

Professor of Biology, University of Saskatchewan,
Saskatoon, Sask., Canada

WILLIS L. TRESSLER, PH.D.

Instructor in Biology, University of Buffalo,
Buffalo, N. Y.

L. R. WILSON, PH.D.

Associate Professor of Geology and Botany,
Coe College, Cedar Rapids, Iowa



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SOME PHYSICAL AND CHEMICAL FACTORS IN THE METABOLISM OF LAKES

By D. S. RAWSON

UNIVERSITY OF SASKATCHEWAN, SASKATOON, SASK., CANADA

INTRODUCTION

THE lake with its plant and animal inhabitants presents a sufficiently unified biotype that it may, with certain reservations, be termed a microcosm. If we consider it as a living unit we may also characterize its complex internal exchanges as metabolism. The biota in question and its activities are to a large extent controlled by physical and chemical influences both internal and external to the lake. It is thus desirable that we should begin with a consideration of these primary physical and chemical factors.

In reviewing so broad a field it has been necessary to select factors which are considered more fundamental and the emphasis is on their interrelations rather than specific effects. The subject of light and the direct influence of various factors on organisms in the lake will be considered in other papers of the series.

THE INTERRELATION OF FACTORS

In approaching the question of physical and chemical factors influencing the metabolism of a lake we might ask certain significant questions. What are these factors? Which of them are most important? Can their separate effects be recognized? How are they interrelated?

In answer to the first question, there are many factors and listing them would serve no useful purpose at the moment. Their relative importance and separate effects will be demonstrated in some measure in our later discussions. With respect to the last question the factors are interrelated in very many ways. The logical relations are so complex that we have been led to construct the accompanying chart (Fig. 1), as a graphic aid to our discussion.

Without considering the chart in detail

you will note in a general way how, starting with geographic location, we have indicated various chains and complexes of factors which have a part in determining the trophic nature and biological productivity of the lake. While the scheme is elaborate it is still not complete. No attempt has been made to indicate the relative importance of particular factors, although something of the sort might be possible with respect to individual lakes rather than for lakes in general. Possibly each investigator should construct his own chart. In any case we think it desirable to visualize something of the maze of relations before entering on the separate discussion of factors as we shall now proceed to do.

THE MORPHOLOGY OF THE LAKE BASIN

The effects of the physical dimensions of a lake on its population and metabolism is a matter of common observation. The fundamental nature of this relation was expressed by Thienemann in 1927 when he demonstrated that the nature of the lake basin and especially its mean depth, was a most important factor in determining lake type. It should be noted, however, that the effects of morphology are often indirect, involving secondary factors such as temperature, oxygen, and the production of nitrogenous materials. The effects may also be greatly modified by the geological nature of the surroundings.

The mean depth of a lake is probably, as Thienemann believes, its most significant dimension. After examining data from many lakes he concluded that most eutrophic lakes had mean depths of less than 18 meters and oligotrophic more; also that the volume of the epilimnion was greater than the hypolimnion in eutrophic and smaller in oligotrophic lakes. In spite of

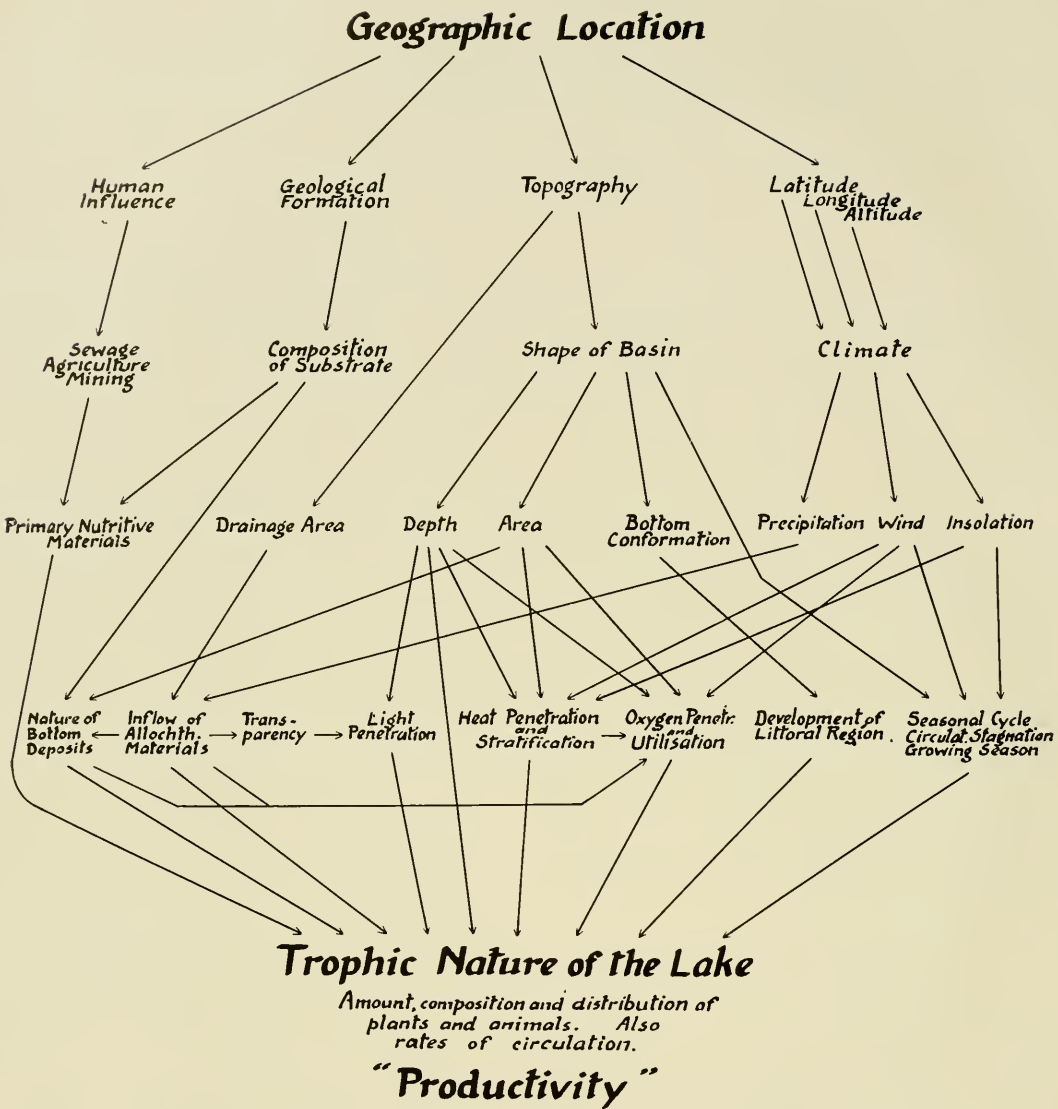


FIG. 1. A chart suggesting the interrelations of factors affecting the metabolism of a lake.

numerous exceptions these conclusions appear to be substantially correct. Ström (1928) and others believe that the relation of water volume to extent of surface and bottom is the most important factor in the development of eutrophy. Mean depth, being a direct indication of this relation, becomes a significant index.

It is not to be expected, however, that a single measure will provide a sure index of eutrophy and oligotrophy. Probably the greatest number of the exceptions in this case will be due to the edaphic factor.

Thus, if a drainage area provides insufficient nutritive salts, a shallow lake may be prevented from developing eutrophy. On the other hand, a deep lake may become somewhat eutrophic if supplied with unusual amounts of nutritive materials. Such exceptions provide practical problems but do not detract from the value of the original thesis.

The area of a lake also affects its metabolism in a number of ways, most directly perhaps through its effect on exposure to wind and consequently on water circula-

tion. In this connection the topography of the surroundings and the shore development (ratio of actual shore length to minimum perimeter for the lake area) are complicating factors. With increase in area the enriching effect of the inshore region is diminished proportionately. Not only are the shore flora and fauna reduced by greater exposure and related factors but the proportion of shore length to total area is rapidly reduced. Finally, the allochthonous materials rich in potential nutrient, are more thinly spread, especially in the open water regions of large lakes.

With area as with depth the effect on life in the lake is produced through a number of secondary and variable factors. Since one could hardly hope to recognize the specific effects of these factors, the writer (Rawson 1930) was led to attempt a demonstration of the total effect of depth and area on the amount of bottom living animals in various lakes. The accompanying graph (Fig. 2) was used to illustrate the result.

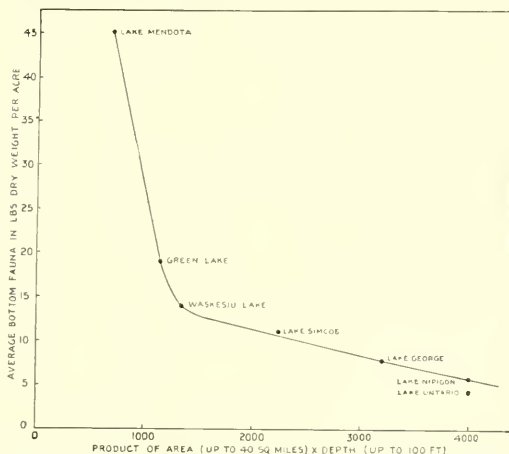


FIG. 2. The quantity of bottom animals as related to depth and area in lakes.

It will be noted that the average weight of bottom organisms per unit area is plotted against the product of depth and area, the latter with certain restrictions. It was believed that the effects of increase were not marked after area reached 40 square miles and depth 100 feet. The whole procedure is rough and the demonstration more qualitative than quantitative. However, the

curve does suggest a correlation between density of bottom population and the product of depth and area. It is also of interest that lakes of a clearly eutrophic nature compose the upper arm of the curve which lies at a considerable angle to the lower arm on which are oligotrophic lakes. Possibly our estimate of the upper limit of the depth effect (100 feet or 32 meters) is too high and the data should be recalculated using Thienemann's value of 18 meters.

The shape or contour of the bottom appears to affect the life in a lake in a way to some extent independent of the above mentioned effects of depth and area. It is clear that a lake with gradually sloping sides will be somewhat richer than one with a steep decline into deep water. This difference between what has been called V-shaped and U-shaped contours may be expressed in various ways. It is commonly indicated by calculating the relative areas of the various depth zones or by constructing a bathymetric curve. Possibly a factor "littoral development" indicated by expressing the area of the littoral zone as a percentage of the total area would be a justifiable innovation, for it appears that the rich flora and fauna of this area are important factors in the production of a lake.

Varying opinions have been expressed as to the significance of the gradient of the lake bottom. Alsterberg (1930) points out the importance of greater or lesser areas of contact between the water and the bottom surface. He even goes so far as to consider this the chief factor in determining oligotrophy and eutrophy. Strom (1930) considers the littoral development of special significance in modifying the trophic condition of a lake. Undoubtedly the U-shaped basin with steep sides is in harmony with other oligotrophic influences and strong littoral development with eutrophy. The question is to some extent related to that of mean depth since in lakes of the same area that with the greater depth will tend to have steeper shores. This should be kept in mind when considering Alsterberg's (1929, 1930) rather violent criticism of

Thienemann's conclusion as to mean depth. The whole question is dealt with thoroughly by Grote (1934, 1934a). We should at least be safe in saying that V-shaped basins and low mean depths are conducive to eutrophy.

Irregularities of bottom conformation have been shown by Welch and Eggleton (1932, 1935) to cause a degree of isolation of submerged depressions within the main basin. The effect of such irregularities on deep currents is little known but must also be of some significance.

THE GEOLOGICAL NATURE OF THE SURROUNDINGS

It is self-evident that the nature of the drainage area must in a large measure determine the kinds and amounts of primary nutritive materials in a lake. The composition, age and weathering of the rock, the soil and vegetation cover, the extent of the drainage area and the amount of run-off are all important considerations. It is perhaps less evident that nutritive materials washed in in this way are not the only determining factors in the biological productivity of the lake. As we have pointed out in the foregoing section, the shape of the lake basin, especially its depth, and the climatic factors affecting water circulation are potent factors in this connection.

The situation was analyzed by Ström (1930) who saw "two great conflicting tendencies: the tendency of each lake to form a microcosm where the evolution of its life processes are determined by the morphology of its basin; and the tendency that works towards making the lakes mere products of their substrates and drainage areas." The same problem was considered by Lundbeck (1934) in his distinction of primary or edaphic oligotrophy from secondary or morphometric oligotrophy, and quite recently it has been further discussed by Hutchinson (1938).

The emphasis which has been placed on the conflict of these influences may have obscured the fact that while they are largely independent they are not necessarily conflicting. The extreme cases of eutrophy

and oligotrophy are usually those in which both edaphic and morphological influences have worked in harmony. When these influences are not in harmony there is often a striking development of eutrophy in spite of surroundings which would normally impose oligotrophy. To cite a single example, Mountain Lake, Virginia, studied by Hutchinson and Pickford (1932), shows a considerable tendency toward eutrophy in spite of a small drainage area and water containing extremely small amounts of salts, nutritive and otherwise.

The question as to which influence is the more important seems to us much like the old question of heredity and environment. The edaphic influences determine the original endowment and the morphology controls later development. Which is the more active can only be decided for particular lakes or regions and there only incompletely. Ström (1930) suggests that Naumann working on lakes in south Sweden was naturally led to overemphasize the importance of edaphic influence while Thienemann working on the distribution of dissolved oxygen was led to exaggerate the importance of morphology. It may be added that Ström himself has made rather complete geological studies in relation to the lakes which he has examined and is, therefore, expressing a well founded opinion.

Our conclusion is that while the edaphic factors determine the kinds and amounts of primary nutritive materials the morphology of the basin and the climate may to a large extent determine the utilization of these materials.

TEMPERATURE

The essentials of the thermal cycle in temperate lakes have long been common knowledge and one speaks glibly of vernal and autumnal periods of circulation and summer and winter stagnation. In intensive work we require a more complete definition of these periods such as has been provided in the discussion of Yoshimura (1935) and further revised by Ricker (1937). In these analyses the four primary periods are subdivided into their complete and partial

phases making in all eight or nine subdivisions.

In practice, observations are rarely so complete as to show the exact limits of these periods. Moreover, in successive years the cycle may vary rather widely; for example, Welch (1935) records a variation of two months in the time of stratification in lakes of northern Michigan. Thus records of both actual and average duration of the periods are desirable and since complete observations over a period of years are available for relatively few lakes, it is the more important that they be recorded and compared. The accompanying chart (Fig. 3), is suggestive of the type of records to

Hutchinson's (1938) calculation of hypolimnial oxygen deficits per day of stagnation may be cited as a significant application of exact data as to seasonal cycles.

The calculation of the amount of heat acquired and lost by a lake during the year was developed by Birge (1916) into a system of comparable heat budgets. His annual heat budget is the amount of heat needed to warm the lake from its winter minimum to the summer maximum and his summer heat income is the amount to raise it from 4° C to the summer maximum. The latter was also referred to as wind distributed heat, but in view of the observations of Ricker (1937) and others as to the depth

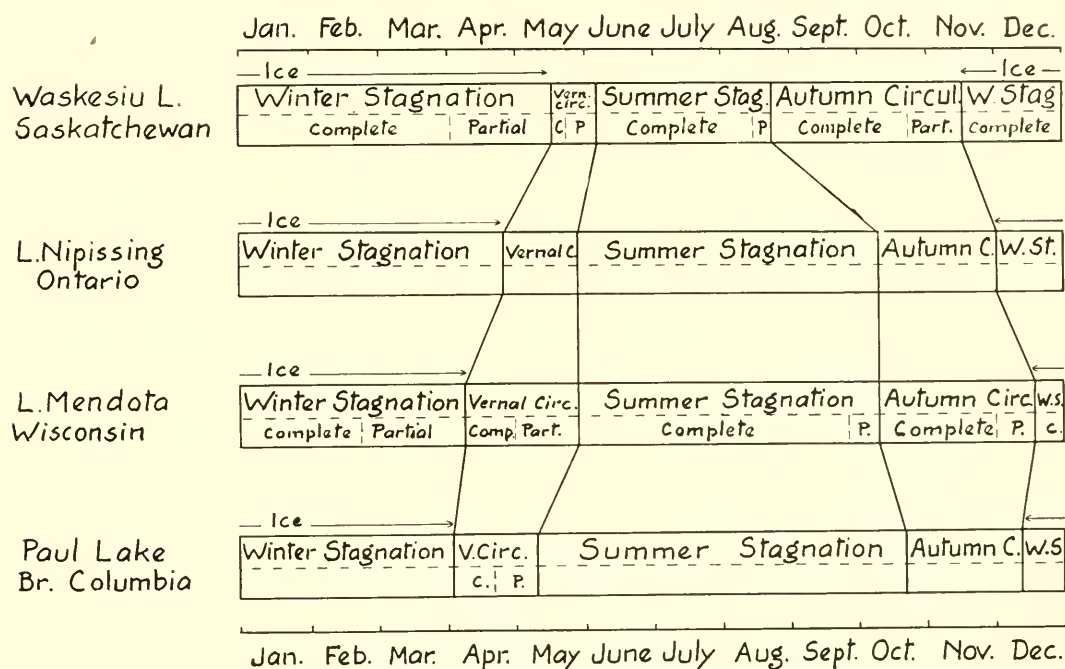


FIG. 3. Comparison of the thermal cycles of four lakes.

which we refer and includes the available data for Waskesiu Lake (Rawson 1936) and three other lakes. In each case the values represent average conditions over a period of at least five years. The periods are those defined by Ricker (1937).

The duration of the periods of circulation and stagnation influences in a profound way the whole ecology of the lake and is of great practical importance in our consideration of the metabolic exchanges.

of direct radiation it might be well to avoid the reference to wind.

Although the heat budget would seem to be a useful means of comparing thermal conditions in different lakes, it has received comparatively little attention. A recent exception to this is Ström (1938) who finds the summer heat income of special use in differentiating mountain lakes from low-land lakes in the same geographic region.

According to Ström (1938), the summer

heat income is only significant in comparing lakes of sufficient depth to store the amount of heat climatically possible. This would restrict its use to lakes of considerable size with mean depths of over 30 meters and in many regions such lakes are rare or absent. It would be more just to say that heat budgets may be more readily compared and interpreted in lakes of more than 30 meters depth but they may be and have been applied to shallower lakes with useful results. It would seem, however, that in the basic question of productivity we are less concerned with the total heat acquired than with the temperature of the trophogenic region (chiefly the epilimnion) and the length of the growing season.

Thermal stratification has been indicated in the foregoing chart of interrelations, as primarily dependent on depth, wind, and insolation. It is also shown as affecting the penetration and utilization of oxygen, thus occupying a central position in the complex of factors which control the internal economy of the lake. Although thermal stratification is one of the most familiar and important of the physical phenomena in lakes, it has still some features which will bear explanation. The warming of the hypolimnion during the summer has been considered by Alsterberg (1930) and Ricker (1937) with the conclusion that in some very clear lakes direct solar radiation must be responsible. As Ricker points out, although the hypolimnion of Cultus lake acquires most of its heat by direct radiation, it is still necessary to assume some mixing (turbulence) to account for its distribution. Karsinkin *et al* (1930) demonstrated that in Lake Glubokoje temperature and oxygen were stratified but not horizontally. Thus turbulence of the horizontal kind proposed by Alsterberg could not have existed. Whitney (1938) in recent studies of transparency in the waters of Wisconsin lakes has shown extensive and irregular microstratification in the thermocline and hypolimnion. The extent of this microstratification would suggest that there is no extensive turbulence in these lakes.

Recently Hutchinson (unpublished note)

has considered the problem of turbulent conduction of heat using the mathematical treatment suggested by McEwen (1931). Analyzing the warming of the hypolimnion in Lake Mendota and Linsley pond, where radiation was known to be negligible, he concludes that in the upper part of the hypolimnion (9 to 15 meters in Mendota) warming is accounted for satisfactorily by the assumption of a constant turbulence in this region. In the lower part of the hypolimnion warming proceeds more rapidly than would be expected. He considers it very unlikely that turbulence could be increased in the lower hypolimnion and suggests that the condition is probably the result of currents near the bottom of the lake bringing bicarbonate, etc., into the water. These currents might not run quite horizontally but would tend to descend slightly along the bank to enter a layer of the same density but of lower temperature. This would provide a means of heat transport other than turbulent conduction. He suggests also that a horizontal current of a few meters per day might account for the above mentioned microstratification effects of Whitney, also for his own observations on alkalinity, and still not be greatly distorted by turbulence of the order which he has calculated for these lakes.

A further observation of great interest has been provided by Welch and Eggleton (1932, 1935) in their work on submerged depressions in Douglas Lake. The temperature curves for seven such depressions showed remarkable differences in stratification in different parts of the same lake.

The direct influence of higher and lower temperature on metabolism is involved in the primary division of eutrophic and oligotrophic lakes. The rapid production in an eutrophic lake is partly dependent on the higher temperatures of its epilimnion. On the other hand, in extreme oligotrophy, *i.e.*, the panoligotrophy of Pesta (1929), the low temperature is a major if not the limiting factor in production. Lundbeck (1934) thinks it is limiting and points to the extremely oligotrophic lakes of the Alps as examples of thermal oligotrophy. Hutch-

inson (1938) does not agree believing that the condition in these lakes is due to chemical factors rather than temperature.

In the foregoing pages we have dealt briefly with what we consider to be the chief physical factors in the metabolism of lakes, excepting of course the extremely important factor of light. We may now turn our attention to certain outstanding chemical factors beginning with the question of dissolved gases.

DISSOLVED OXYGEN

In temperate lakes the supply of oxygen is largely renewed during the vernal circulation. When thermal stratification appears the amount of oxygen in the hypolimnion begins to decrease and as stagnation advances it may disappear from the whole of this region. In the thermocline there may be a sharp increase or decrease in dissolved oxygen and in the epilimnion it remains relatively high all summer. With the autumn turnover and circulation the oxygen of the deep water is restored, although it may be depleted once more in a winter stagnation period under the ice. Among these changes in the distribution of oxygen, we find the summer depletion in the hypolimnion of greatest significance in the metabolic activities of the lake.

Thienemann (1928) developed a number of standards or values for the comparison of amounts of oxygen in lake waters. Various investigators took up the problem and a long series of papers has appeared, many of them controversial. The result has been an improvement in the treatment of the physical data and the demonstration that certain of the early standards or indices were of little use. Thus Thienemann's expression

$\frac{O_2H}{O_2E}$ indicating the ratio of the total oxygen of the hypolimnion to that of the epilimnion is found somewhat unsatisfactory. It may give misleading results especially in oligotrophic lakes with small hypolimnia. It would seem also that the oxygen deficit of the epilimnion or any index involving this calculation is of little significance as long as the amount of oxy-

gen released by photosynthesis remains an unknown quantity. Thus the hypolimnial deficit is the more widely used.

Alsterberg (1930) improved the expression of oxygen deficits when he calculated his so-called "absolute deficit." Maucha (1931) and Ricker (1934) carried the considerations still further. Ström (1931) considered that the deficit should be expressed per unit area of the hypolimnion in oligotrophic lakes and per unit area of lake in eutrophic. Grote (1934, 1934a, 1936) has considered the problem minutely and has shown the deficit to be of very complex origin. Hutchinson (1938) agrees with Ström as to the necessity for relating deficits to area of the hypolimnion. In the case of lakes where the oxygen of the hypolimnion is completely exhausted he suggests that the "real" deficit can be obtained by adding to the apparent deficit the amount of oxygen necessary to oxidize the existing quantities of such substances as methane and hydrogen sulphide, substances which would not have formed in the presence of abundant oxygen. This procedure seems to be logical but the data are not often sufficiently complete to make it practical. It is also a question whether this correction goes far enough, for there must be dead plankton, bottom detritus, and other materials which would have been decomposed using additional amounts of oxygen had they been available. A noteworthy feature of Hutchinson's calculations is the expression of hypolimnial deficits *per day*, recognizing the desirability of including the time factor and dealing with rates rather than standing quantities.

The interest in expression of hypolimnial oxygen deficits arises from the possibility of their use as a measure of lake productivity. The basic assumption was that much of the organic material produced in the trophogenic (photosynthetic) region of a lake sinks into the deeper water, the tropholytic or decomposition zone where it is oxidized. This assumption has been seriously questioned. Alsterberg (1927) proposed that the chief consumption of oxygen was in the bottom deposits and that the

reduction throughout the hypolimnion was produced by contact with the bottom layers through the agency of hypolimnial water movements, *i.e.*, turbulence. It has also been demonstrated by Rossolimo and Kusnezowa (1934) that in some lakes the bacterial oxidation of gases such as methane and hydrogen may be responsible for much of the oxygen reduction. These gases were produced by decomposition of the bottom ooze and passed upward into the hypolimnion. There is probably some truth in each of these explanations but we are not yet able to estimate their relative importance in the major problem. In each case the utilization of oxygen was accomplished through the agency of bacteria. Recent studies have demonstrated large numbers of bacteria in the lake water, *e.g.*, Kusnetzow and Karsinkin (1931). In view of the large numbers of bacteria in the hypolimnion, there would seem to be greater possibility that the original explanation was the correct one, *i.e.*, that hypolimnial consumption of oxygen is largely due to decomposition of dead plankton falling through the hypolimnion. We need to know, however, whether these bacteria are promoting oxidative decompositions and to what extent they are acting on organic matter or on the above mentioned gases.

Even if the hypolimnial deficit should be reasonably established as an index of production there are several factors which hinder or prevent its use in particular lakes. If appreciable amounts of allochthonous organic materials are present in the lake water the utilization of oxygen in the decomposition of these materials is a disturbing factor of unknown extent. Thus in cases where such dystrophic influences are demonstrated or suspected we should not attempt to apply the oxygen indices.¹ There are also some lakes in which there is an appreciable production of oxygen in the

hypolimnion by photosynthesis. In Crystal Lake, Wisconsin, Juday and Birge (1932) found a high transparency in the water and a green plant living on the bottom at a depth of 20 meters, while in Crater Lake, Oregon, Hasler (1938) records green aquatic mosses from a record depth of 120 meters. Again, as Ström (1931) points out, the hypolimnial deficit ceases to indicate production in extremely eutrophic lakes where the hypolimnial oxygen is exhausted and is of doubtful value in extremely oligotrophic lakes where the deficit is very slight. Hutchinson (1938) has attempted to meet the former objection by the calculation of his real deficit as described above. Finally, the consumption of oxygen by respiration may at times have a significant effect on the oxygen deficit, as in the case of Lake Nipissing (Fry 1937) where a large population of ciscoes is crowded into a restricted hypolimnion.

From the foregoing discussion it would seem almost impossible to justify on theoretical grounds the use of the hypolimnial deficit as a measure of production. Nevertheless, in the practical field we find it used with apparent success by Hutchinson (1938). He has demonstrated that, applied with care and discretion, it works both in comparing productivity between individual lakes and as an indication of the character of lakes in a particular district.

Having considered the question of hypolimnial oxygen deficits to this length, we might conclude that, although they are not easy to apply and subject to certain limitations, they are of definite value qualitatively and to a lesser extent quantitatively.

In considering the controversial question of oxygen as an index to lake metabolism we must not neglect its direct effect on the life of the lake through its availability for respiratory requirements.

In the epilimnion of a lake, because of wind-caused renewal and photosynthetic production, there is usually an abundant supply of oxygen for respiratory needs. In the hypolimnion we find a reduction in the amount of oxygen varying from a slight deficit to complete absence as described

¹ Nevertheless Lommerblad (1931) considers Thienemann's calculations applicable to dystrophic lakes which he studied, and Ström suggests that the hypolimnial deficit may be used but should be expressed per unit of volume rather than of area. Presumably these authors are not using the deficits as indicating production.

above. In the thermocline the quantities of oxygen show considerable differences. The thermocline minimum or oxygen notch has been observed frequently and at the other extreme Juday and Birge (1932) have demonstrated an excess of oxygen in some cases amounting to extreme supersaturation. The excess is accounted for by active photosynthesis of the phytoplankton, but the complete explanation of the thermocline minimum is not yet available. Most explanations assume that the dead and dying plankton sinking from the epilimnion tend to linger and accumulate in this zone and that the notch indicates the decomposition of this material. The use of oxygen for respiration by zooplankton is undoubtedly involved but it is considered inadequate (Naber 1933) to account for the minimum. To explain the delay in the sinking of organic material, Birge and Juday (1911) have cited the sharp decrease in temperature and resulting increase in density at this level. Antonescu (1931) discusses the effect of currents on sinking bodies and thinks the delay related to the "minimum turbulence" in the thermocline.

Considering the distribution of dissolved oxygen in the three regions it may be assumed that it is rarely a limiting factor for distribution or production in the epilimnion, that it may operate in an irregular way in the thermocline, and that in the hypolimnion the deficiency of oxygen frequently tends to drive out certain animal forms.

Field observation of the effects of lowered oxygen on animal distribution has been extensive, but unfortunately it is often impossible to separate the effects of oxygen shortage from those of other factors, for example, increased carbon dioxide or hydrogen sulphide. In some cases the distribution of fish seems to give clear-cut evidence of degrees of oxygen tolerance, for example, the distribution of the lake trout in lakes of Prince Albert National Park, Saskatchewan (Rawson 1936). In the pioneer experiments of Smith (1925) in Douglas Lake, the experimental fish failed to live below the thermocline where the

oxygen was severely reduced. As he points out we do not know whether lack of oxygen was the only or just the chief factor. Scott (1931) describes the cisco in Indiana lakes as forced up by oxygen depletion and trapped beneath the still lower concentrations of a thermocline minimum. Fry (1937) attributed the upward migration of ciscoes in Lake Nipissing to the combined effect of lowered oxygen and increased carbon dioxide. However, in view of the effect of high carbon dioxide on the buoyancy mechanism of certain fishes (Hall 1924, Fry *et al.* 1937), it is possible that the upward migration is more closely related to the increase in carbon dioxide tension which is concomitant with the lowering of oxygen in the hypolimnion.

In cases of extreme stagnation the effects of hydrogen sulphide may be added to those of high carbon dioxide and low oxygen. In Pinantan Lake, observed by the author (Rawson 1934), there was no oxygen below the thermocline. The fish (trout) had moved out and even the oligochaetes, chironomid larvae, and pisidia, normally resistant to lowered oxygen, were absent from the bottom of the hypolimnion. It is probable that the hydrogen sulphide present was in some measure responsible for the formation of what Welch (1935) terms a "biological desert" below the thermocline.

In suggesting that further work is needed in the field we should mention also certain experimental work which has shown interesting possibilities. Powers (1934) has indicated the possible nature of the effect of free carbon dioxide on the ability of haemoglobin to acquire oxygen. Langford (1938) drew certain conclusions as to the effect of dissolved oxygen, carbon dioxide, and temperature on migration of entomostraca in Lake Nipissing. He then tested these conclusions in the laboratory using apparatus devised by Fry to reproduce in miniature the gradients observed in nature and was able to some extent to verify his first theories. A comparable device for laboratory studies has been described recently by Schwabe (1937).

The differences in the oxygen require-

ments of lake organisms have been studied both in laboratory and in the field. As Welch (1935) points out, most aquatic organisms appear to have a high tolerance for excess oxygen. At the other extreme there is a considerable group of bottom animals which survive for long periods in water containing no oxygen. Other organisms, for example, fish, are affected adversely by rather low concentrations. In this connection we should recall Ruttner's (Brehm and Ruttner 1926) effort to recognize the effect of temperature on the oxygen requirements of aquatic organisms by calculating "respiratory values." Ricker (1934) mentions both the value and limitations of this procedure.

CARBON DIOXIDE

Carbon dioxide occupies an important place in the transfer of materials that we describe as the metabolism of a lake. It is an essential substance for photosynthesis and thus stands at the threshold of all production. The forms and quantities in which it occurs and its combinations with calcium have been the subject of much study. Pia (1933) provides a recent and rather complete discussion and various authors including Juday *et al.* (1935) have published the results of extensive field studies.

The free carbon dioxide in the surface water of a lake varies rather widely according to photosynthetic activity of its phytoplankton. If the lake is thermally stratified there is usually a considerable increase in the hypolimnion. Bound carbon dioxide is usually more constant with only a slight increase near the bottom. The phytoplankton is able to use in photosynthesis both the free carbon dioxide, the "half-bound" part of the bicarbonates, and even some of the monocarbonates if necessary. When the half-bound carbon dioxide is used the monocarbonate may be precipitated and sinks to the bottom or it may be redissolved in the hypolimnion if there is free carbon dioxide present in that region. Since carbon dioxide is used in the assimilation of bacteria as well as in green plants and since it is produced by animal respiration, we should re-

gard the amount present as a "balance on hand" depending on the various rates of transfer.

Apparently the total carbon dioxide available for photosynthesis is seldom low enough to make it a limiting factor for production of phytoplankton. That it may have some limiting effect is suggested by evidence from the work of Birge and Juday (1911) that phytoplankton is unusually poor in soft water lakes of Wisconsin. In lakes of northeastern Indiana, Scott (1931) reported a correlation between the quantities of carbonates and numbers of diatoms but not with numbers of blue-green algae. Hile (1936) suggests that the amount of bound carbon dioxide in lakes of northeastern Wisconsin was directly correlated with the density of cisco populations and inversely with their growth in weight. He suggests that the amount of bound carbon dioxide is roughly indicative of the productive capacity of a lake but his data provide little support for this assumption. It is noteworthy that he finds the amount of surface plankton not related to production of ciscoes and cisco growth poorest in the most eutrophic lake.

The presence of large amounts of free carbon dioxide may be a direct factor in limiting the distribution of aquatic animals. As in the case of oxygen, increased carbon dioxide is accompanied by changes in other factors so that the specific effects are difficult to establish. It seems probable that some organisms show a negative reaction to increased carbon dioxide even though the amounts are by no means toxic, a condition which rarely occurs in nature. Powers (1934), as cited above, has investigated the toxic effects of carbon dioxide on fishes and suggests that sudden increases have a pronounced effect on the respiration of fishes. More recently Powers (1938) and also Fry and Black (1938) have shown how carbon dioxide affects the level to which oxygen can be removed from the water by fish.

HYDROGEN ION CONCENTRATION

The trend of opinion in recent years suggests that the pH of the aquatic environment is of less importance as a limiting

observation that if there are no macroscopic lime encrustations visible (on plants, etc.) the water is poor in calcium, if visible medium, and if abundant encrustations and concretions the lake is rich in calcium.

The significance of calcium content with respect to trophic condition and the classification of lakes has been much discussed. The typical eutrophic lake is rich in calcium and the typical oligotrophic lake usually poor. However, Ström (1928) pointed out that certain oligotrophic lakes in the Alps were rich in calcium and he proposed a subdivision of each of the primary types into calcium rich and calcium poor divisions (Fig. 5). Ohle (1934) has since

nitrates usually less than 0.5 mg per liter, nitrites less than 0.1 and ammonia also scarce but capable of considerable increase if oxygen is reduced. Changes in seasonal and vertical distribution are so marked that extensive sampling is required. After the usual maximum in late winter, vernal circulation brings about a fairly uniform distribution and then the phytoplankton in the upper layers begins to reduce the supply. Dead organisms sinking and decomposing increase the amounts near bottom until at midsummer nitrates near bottom are often several times that at the surface. Nitrites and ammonia may also be concentrated at the bottom and are frequently absent at the surface. Autumn circulation again restores uniform distribution and the decomposition of the summer "crop" of organisms begins to increase the inorganic nitrogen again toward the winter maximum. The extent of stratification and variation of inorganic nitrogen has been demonstrated by Yoshimura (1932), by Juday *et al.* (1938), and by others. A fuller explanation of these changes in terms of water movements, the activities of green plants and bacteria lies beyond our scope.

The average amounts of phosphorus in natural waters is usually less than .05 mg per liter and thus much less than those of nitrogen. During the summer there is often a marked increase in the phosphorus of bottom water and sometimes but not always a decrease at the surface (Juday and Birge 1931). The cycle involving concentration near bottom and subsequent distribution by water circulation is similar to that of nitrogen. Certain European investigators have given their attention recently to the loss of phosphorus from circulation either temporarily by adsorption to colloidal humous material (Ohle 1935, Gessner 1934), or permanently by precipitation as iron phosphate (Einsele 1936, 1938). The adsorption of phosphate to iron hydroxide is suggested by Gessner (1934a) as causing a physiological scarcity of phosphates.

The small quantities of nitrogen and phosphorus in lake waters, their variability and the technical difficulties of their deter-

	+(N+P). Fundamenteally Eutroph.		-(N+P). Fundamenteally Oligotroph.	
	+Ca.	-Ca.	+Ca.	-Ca.
+Humus ...	Not investigated and probably not existing	"Humusschlamm-seen." Humic mud lakes.	? Dystroph lakes in Scotland and Eugen.	* Dystroph.
-Humus ...	Eutroph.	Not yet investigated, but almost certainly existing.	A. Oligotroph lakes in the Alps.	* B. Oligotroph Norwegian lakes.

FIG. 5. Calcium and humus in the division of primary lake types. (From Ström, 1928.)

reported lakes in northern Germany entrophic but poor in calcium. Naumann (1932) terms certain oligotrophic lakes of the Alps rich in calcium "alkalitrophic," an opinion with which Thienemann (1933) strongly disagrees.

NITROGEN AND PHOSPHORUS

Nitrogen and phosphorus are raw materials for protein synthesis and thus stand in a position as important as that of carbon dioxide in photosynthesis. It would seem that a study of the availability of nitrogen and phosphorus should be a direct approach to the evasive problem of productivity but the approach has many obstacles. It is difficult to obtain satisfactory determinations of the amounts available; our knowledge of the role of bacteria in the cycle is incomplete and the greatest difficulty is our inability to measure the rates of transfer and utilization.

The amounts of inorganic nitrogen in natural waters are relatively small with

mination have been obstacles in the development of this important field. Recent improvements in chemical technique have opened up new possibilities. To cite a special case, Strom (1933) has applied the method used in marine waters by Schreiber (1927). It consists of a direct evaluation of the nitrogen and phosphorus in lake waters by their effects on pure algal cultures. The method is slow and laborious. Its final utility cannot be predicted but its directness has a strong appeal to the ecologist.

In field studies it is frequently impossible to have the analyses which might be desired and as Strom (1930) points out we may look for evidence of the nitrogen and phosphorus factor in its effects, for example, on the oxygen curve. Naumann (1932) also discusses how the nitrogen and phosphorus standard may be inferred from the phytoplankton and other indices of the economy in the lake. Such inferences were the basis for the original separation of eutrophic and oligotrophic lake types. In some cases the inferences may be better than the actual measurement for the amounts present may differ greatly from those available. Ruttner (1937) shows that in some lakes in the Alps without complete circulation there are large amounts of nitrogen and phosphorus which are not available for production. The aforementioned physiological scarcity of phosphates is also a case in point.

Nitrogen and phosphorus are frequently cited as limiting factors in plankton production and apparently they may be in some cases. In the more exact studies it has often been impossible to show that either was limiting. Atkins (1926) discussing the data from Wisconsin lakes finds "a complete absence of any evidence that in the water of these lakes a deficiency of nitrogen acts as a factor limiting the plankton." Wiebe (1931b) concludes that nitrates and ammonia are not limiting in the Mississippi river. It is of course difficult to decide just when a factor becomes limiting. Rice (1916) suggests that in Winona Lake, Indiana, plants flourished in water with extremely small amounts of nitrates and

nitrites when conditions for producing these materials were favorable.

Phosphorus as we have noted is usually present in smaller quantities and has been more frequently considered a limiting factor for phytoplankton, *e.g.*, by Atkins (1926), Strom (1931), Yoshimura (1932), and Gessner (1934a). However, when Juday *et al.* (1928, 1931) investigated the question in a large number of lakes in Wisconsin they found no correlation and only slight reduction of the phosphates in the upper water, although large crops of phytoplankton had been produced. Ricker (1937) found similar quantities of phosphorus and only slight variation in Cultus Lake, British Columbia.

IRON

The necessity of iron for plant growth is undoubted though its physiological role is still uncertain. It probably acts as a catalyst in the formation of chlorophyll and may be also involved in respiratory activities. Strom (1928) and Ohle (1934) mention it as a probable limiting factor for phytoplankton growth in some lakes. Naumann (1932) emphasizes its significance by creating a "siderotrophic" water type, a subdivision of the oligotrophic, "in which the iron spectrum reaches an important level."

The amount of iron present in surface waters of lakes is usually less than 2.0 mg per liter but it may be much more abundant, especially in the bottom water. Manganese in the same waters usually occurs in smaller quantities, but Ohle (1934) finds that manganese is more abundant than iron in humous lakes. It has been suggested that manganese may under certain conditions serve as a partial substitute for iron. Strom (1933) found that in some of his algal cultures this was not the case.

Recently Hutchinson *et al.* (1938) have shown that in certain lakes of Connecticut and New York the amount of ferrous iron in solution in the hypolimnion determined the value of the redox or oxidation-reduction potential. Moreover, there was a close correlation between these potentials and the occurrence of the larvae of various genera

of chironomids so commonly used as indicators of trophic condition. The authors point out the uncertainty as to the relative significance of redox potential and oxygen content in affecting the distribution of these larvae, but one might expect the potential to provide a useful index to the hypolimnial and benthic environments.

Another special way in which iron enters into the chemical economy of the lake has been mentioned above where the presence of iron hydroxide in the deeper water results in adsorption and precipitation of phosphates thus removing them from circulation.

SILICA

Silica in the surface waters of lakes is highly variable but usually less than 10 mg per liter. Stratification is frequent and the bottom water may contain twice that of the surface.

The variation in silica content has been compared with the amount of diatoms produced both in marine and fresh waters. Atkins (1926) finds no proof that silica is ever a factor limiting diatom production in the ocean. Meloche *et al.* (1938) observed certain correlations between silica and diatoms in Lake Mendota but concluded that several factors were involved. Since the silica content did not fall below .13 mg per liter it was presumably not limiting. Ricker (1937) found 6.0 mg of silica per liter in water of Cultus Lake and calculated that this was about 25 times the amount of silica represented by diatoms at the time of their maximum abundance.

ORGANIC MATERIALS

In the foregoing discussion the treatment of chemical materials has been arbitrarily limited to their mineralized state. Some of these materials are being built up into living matter and returned to the mineral state. Thus in the economy of the lake we must consider also the materials represented by living organisms and by the dead organic matter at various stages of destruction.

The origin of the non-living organic matter is twofold. From the point of view of

productivity we have special interest in those produced within the lake (autochthonous) by the death of organisms or as physiological wastes. Organic materials of external (allochthonous) origin are introduced from the surrounding terrain chiefly by drainage or seepage. Unfortunately in practice the two can not be so readily separated.

Birge and Juday (1934) have indicated that the dissolved (non-centrifugable) organic material in Wisconsin lakes to be composed of about 75 per cent carbohydrates, 25 per cent proteins, and a very small quantity of fats. The carbon to nitrogen ratio was approximately 12 to 1. The same authors found that in lakes with a minimum of allochthonous materials the total organic (dissolved and particulate) material was about 4 mg per liter, of which the plankton represented approximately 16 per cent. In the average of their lakes they found 16 mg of which plankton was 8 per cent, and in lakes rich in extractives 50 mg and plankton 4 per cent.

Assuming the existence in most lakes of an amount of dissolved organic material possibly seven times as great as that of the plankton, the question arises as to how and to what extent this is made available for the production of living organisms. Presumably the chief factor is the action of bacteria in breaking it down into nitrates and ammonia. The study of lake bacteria is advancing rapidly and we can soon hope for more light on this question. A second activity, the direct utilization of dissolved organic materials by lower plants and animals is still debatable. It seems probable from the work of Krogh (1931) that such utilization occurs but is of little importance. Nevertheless, as Varga (1934) indicates, we cannot exclude it as a factor.

That the dissolved organic materials are by no means equally available in different lakes is apparent from their abundance in lakes strongly affected by dystrophy and producing relatively smaller amounts of plankton. In such lakes (with color 130–268 U. S. Geol. Sur. scale) Birge and Juday (1934) found the plankton as low as 3 per cent of the total organic material while in

uncolored lakes, *i.e.*, those with little allochthonous materials, the percentage was as high as 23. We may point to this as a demonstration of dystrophy as a disturbing element in the metabolism of lakes. It cuts across the normal gradation from entrophy to oligotrophy and thus should not be considered as indicating a third lake type. It has been suggested that these organic materials of allochthonous origin not only fail to support production but they may actively inhibit production by adsorbing inorganic materials, *e.g.*, phosphorus, of nutritive importance.

The comparative constancy of dissolved organic materials in lakes is in striking contrast with the high variability of the same elements in their inorganic state. Birge and Juday (1927) found little correlation between amounts of the two groups of substances except in lakes where both were present in very small quantities. A part of this constancy may be apparent rather than real since the quantities of organic materials are much larger than the

inorganic and the metabolic exchanges make lesser inroads into this large capital.

The immediate temptation is to hope that the dissolved organic matter will provide an index to productivity. This could only be considered in lakes where the dystrophic factor is known to be at a minimum. Even in these cases we still face the objection that productivity must be determined not by the amount of organic capital but by the rate of turnover. Our final statement is that which Birge and Juday have made on various occasions. We do not know the function of the dissolved organic matter in the biological economy of the lake.

CONCLUDING REMARKS

Our discussion began with an attempt to organize the physical and chemical factors in the metabolism of a lake and a chart (Fig. 1) is presented to suggest these interrelations. As a second step we have considered a number of these factors summarizing and attempting to evaluate present knowledge in this field. In doing so we

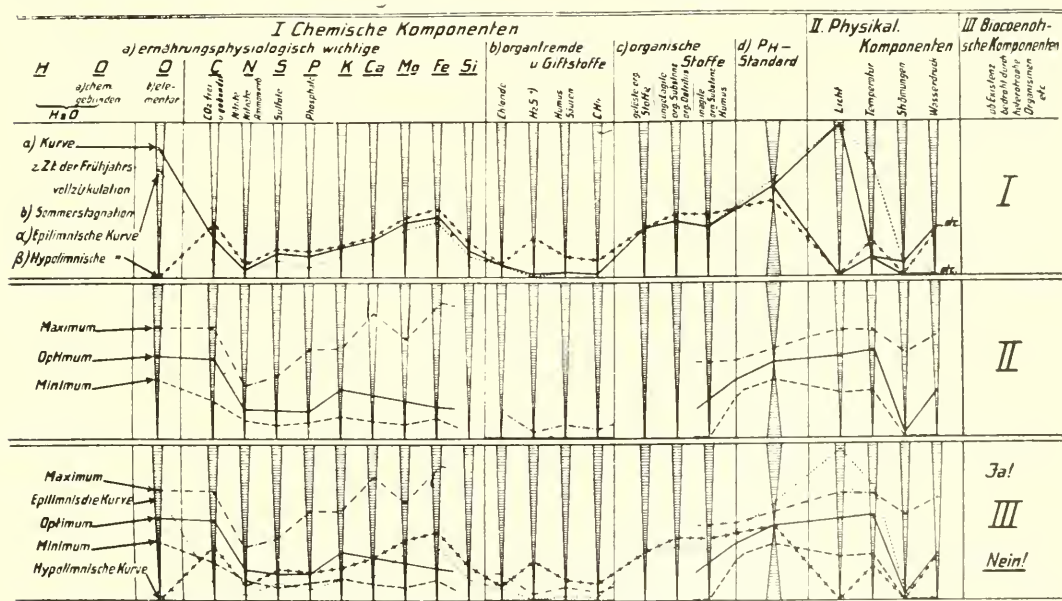


Fig. 1. Ökologisches Totalspektrum (Theoretisches Schema).

Oben: Milieu eines Biotops

a) zur Zeit der Vollzirkulation,

b) während der Sommerstagnation, { a) Epilimnische Kurve,

β) Hypolimnische Kurve.

Mitte: Valenzspektrum eines autotrophen planktischen Organismus. — Unten: Beide Spektren (Milieu während der Sommerstagnation) kombiniert. — Weiteres s. Text!

Fig. 6. The ecological total spectrum of Grote (1934).

have in some measure answered our questions as to which are most important and to what extent their separate effects can be recognized. We may now ask what general conclusions or picture of the whole field can be offered.

The number of environmental factors involved makes it difficult to bring them into a single picture. However, Grote (1934) has made a noteworthy attempt to do this in his ecological total spectrum (Fig. 6). It will be noted that he lists the factors and attempts to show the condition with respect to each at the time of vernal circulation and during summer stagnation. In the central section he indicates the optimum and limiting conditions for an autotrophic plankton organism. In the lower section he superimposes the upper curves. The procedure is highly theoretical but it merits careful consideration. However, it is our contention that these factors do not act independently and we must look to another field for a natural synthesis of our conclusions.

A proper scheme of lake types should provide a logical grouping of lakes with respect to these factors. On a basis of the material discussed above we feel that there are only two valid lake types, eutrophic and oligotrophic, and these intergrade. Dystrophy is considered as a disturbing factor which may affect the natural gradation from eutrophy to oligotrophy at any point. Certain features such as shallowness, smaller area, V-shaped bottom contour, higher temperature, and plentiful supplies of nitrogen, phosphorus and calcium have been indicated as conducive to eutrophy while greater depth, larger area, U-shaped bottom contour, lower temperature and lesser supplies of nitrogen, phosphorus and calcium tend to produce oligotrophy. If in any lake, all factors are favorable (harmonious), extremes of eutrophy or oligotrophy will result. In most lakes the degree of eutrophy or oligotrophy represents the balance of certain favorable factors over others of an unfavorable (disharmonious) nature.

In a survey such as this, it is considered fitting to suggest problems or fields in which there is urgent need for research.

This has already been done, to some extent, by reference to the numerous unsolved problems and it may be presumptuous to make more specific suggestions. Personally we are impressed with the need for studies of the various activities of lake bacteria, the role of organic matter in lake water and the question of deep water currents. No doubt these and other gaps in our knowledge are evident to most limnologists who merely await the opportunity to attack the problems involved.

Emphasis might be placed on the desirability of certain attitudes in research in this field. Ström and others have urged the need for a more dynamic view, to consider the time factor and rates of production rather than static conditions and absolute amounts. Such an attitude is particularly needed in that most difficult of all limnological problems, productivity.

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THE UTILIZATION OF SOLAR ENERGY BY AQUATIC ORGANISMS

By GEORGE L. CLARKE

BIOLOGICAL LABORATORIES, HARVARD UNIVERSITY, CAMBRIDGE, MASS., AND WOODS HOLE OCEANOGRAPHIC
INSTITUTION, WOODS HOLE, MASS.*

My first object in this paper is to present a brief summary of our present knowledge of the availability of radiant energy in natural waters and the utilization of it by aquatic animals and plants. My more important desire in bringing together this material, however, is to delineate the critical problems which have now arisen on this subject and upon the solution of which further significant progress depends. Research in this field falls roughly into two parts, namely, (1) the determination of the amount and nature of the light actually present at various depths in all types of water bodies, and (2) the measurement of the extent to which submerged organisms are able to utilize the light present. From the biological point of view we need to know not only the range of light intensity at any point but also its spectral composition, its angular distribution, and its distribution in time.

The solar energy which falls upon a body of water is subject first of all to a "surface loss" which in the case of the ocean may amount to as much as 60 per cent in rough weather. Only about 3 to 9 per cent of this is ordinarily due to reflection (for solar altitudes greater than 30°) and the remainder has been found to be caused by a greatly increased rate of extinction in the uppermost meter of water (Powell and Clarke 1936). It was originally suggested that this effect was due to bubbles existing near the surface but this explanation has been questioned by Poole (1938). Whether a similar increase in extinction coefficient of the subsurface stratum occurs in lakes at times when waves exist is a question which invites investigation.

As the light passes from the surface

downward into the water, it is reduced in intensity according to the following equation:

$$\frac{I}{I_0} = e^{-kL}$$

where I_0 is the initial intensity, I is the final intensity, k is the extinction coefficient, L is the thickness of the layer in meters,† and e is 2.7. When this relationship between the reduction in the light and the thickness of water through which it has passed is expressed graphically on a semilogarithmic plot, a straight line is obtained (Fig. 1). The slope of the line is determined by the value of the extinction coefficient, k , which is thus an index of transparency. The extinction coefficient varies widely in the different parts of the spectrum—even for pure water—and its actual value depends upon the precise wavelength considered. In Fig. 1 the rate of absorption of red light by distilled water is seen to be very high, that for yellow light lower, and that for blue light very much lower. For example, after traversing 70 meters of distilled water blue light has suffered only a slight reduction to 70 per cent of its initial value, whereas yellow light has been reduced to 6 per cent. In the case of red light a reduction to 6 per cent has already taken place after passing through less than 3 meters of water.

Now the energy of the sun as it reaches the surface of a natural body of water is not equal in all parts of the spectrum but is distributed as shown by the uppermost curve in Fig. 2. We therefore start with

† This quantity may be taken as the depth, but if the mean path of the light departs from the vertical, as is usually the case in natural waters, a small correction is required since the path length is then greater than the vertical depth (*cf.* Whitney 1939).

* Contribution No. 201.

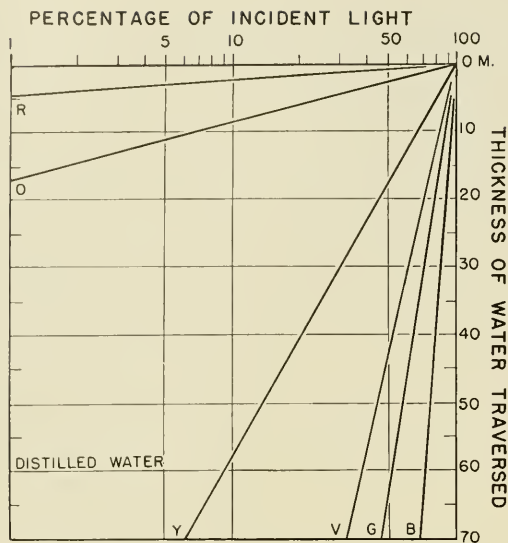


FIG. 1. Transmission of light by distilled water at 6 wave lengths within the visible spectrum. Curves show the percentage of incident light (logarithmic scale) which would remain after passing through the indicated thickness of water.

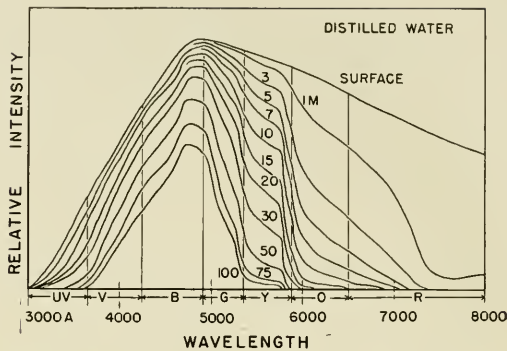


FIG. 2. The spectral distribution of solar energy at the earth's surface is given by the uppermost curve. When sunlight is passed through successive meters of pure (distilled) water, the reduction of intensity and the change in spectral distribution which result are indicated by the curves beneath (from Birge and James 1939).

fraction of the whole. As a consequence, after sunlight had traversed 100 meters of distilled water nothing but the blue component with a little green and violet would remain, as is demonstrated by the family of curves in Fig. 2. These curves represent the uppermost limit possible for the transparency of any body of water.

In most natural waters the rate at which light penetrates is further decreased by the presence of varying amounts of suspended particles and dissolved material. The great diversity which results in the transparency of natural waters may be appreciated by comparing the curves of light penetration for certain typical lakes and oceanic areas in various parts of the world (Fig. 3). As will appear presently, only those measurements can be fairly compared which were made within the same part of the spectrum. In the figure observations with photometers sensitive to the yellow-green region (maximum 5500Å) are presented. Sargasso water is seen to be nearly as transparent as distilled water in this spectral region and light is reduced to 1 per cent of its surface value at about 100 meters. Beyond the edge of the continental shelf 100 miles or more from the coast in both the Atlantic and the Pacific the transparency is such that the 1 per cent value is reached at about 50 meters. In coastal waters the same value occurs at between 30 and 15

Color	Wave length ¹	Absorption per meter ²	Extinction coefficient ³
	Å	per cent	
Red	7200	64.5	1.1
Orange	6200	23.5	0.27
Yellow	5600	3.9	0.040
Green	5100	1.1	0.011
Blue	4600	0.52	0.0052
Violet	3900	1.63	0.016

¹ Mean wave length of range for each color as employed by Birge and Juday (1931).

² As determined for the designated wave length by James and Birge (1938).

³ Extinction coefficient = k in the equation $I/I_0 = e^{-kL}$ where the light is reduced from I_0 to I by a stratum L meters thick. $e = 2.7$.

unequal quantities of energy at the different wavelengths and these are absorbed at unequal rates as the light penetrates into the water. The result is that after passing through successive meters of water the spectral composition of the light present becomes rapidly and profoundly altered. The infrared and red components are reduced to small quantities within a very few meters and the ultraviolet, which was initially of small magnitude, soon drops to a minute

meters. Although there are a few inland lakes which are as clear as typical coastal waters, the majority of them are more turbid.* In Midge Lake, for example, the illumination has been reduced to 1 per cent

*A recent measurement in Crater Lake, Oregon, (Hasler 1938) yielded a depth of 40 meters for the visibility of the Secchi disc. The clearest lake which had been investigated previous to this observation was Crystal Lake, Wisconsin, in which the Secchi disc was found to disappear at about 15 meters. The transparency of Crater Lake, there-

of its surface value at 3 meters. The extreme range of possible transparency in natural waters is thus very great.

In the various natural waters we find that the *relative* rates of absorption of *different parts of the spectrum* are not the same as those characterizing distilled water. This situation is brought about by the fact that both the suspended and the dissolved

fore, greatly exceeds that of any other lake in which measurements have been made.

PERCENTAGE OF SURFACE LIGHT

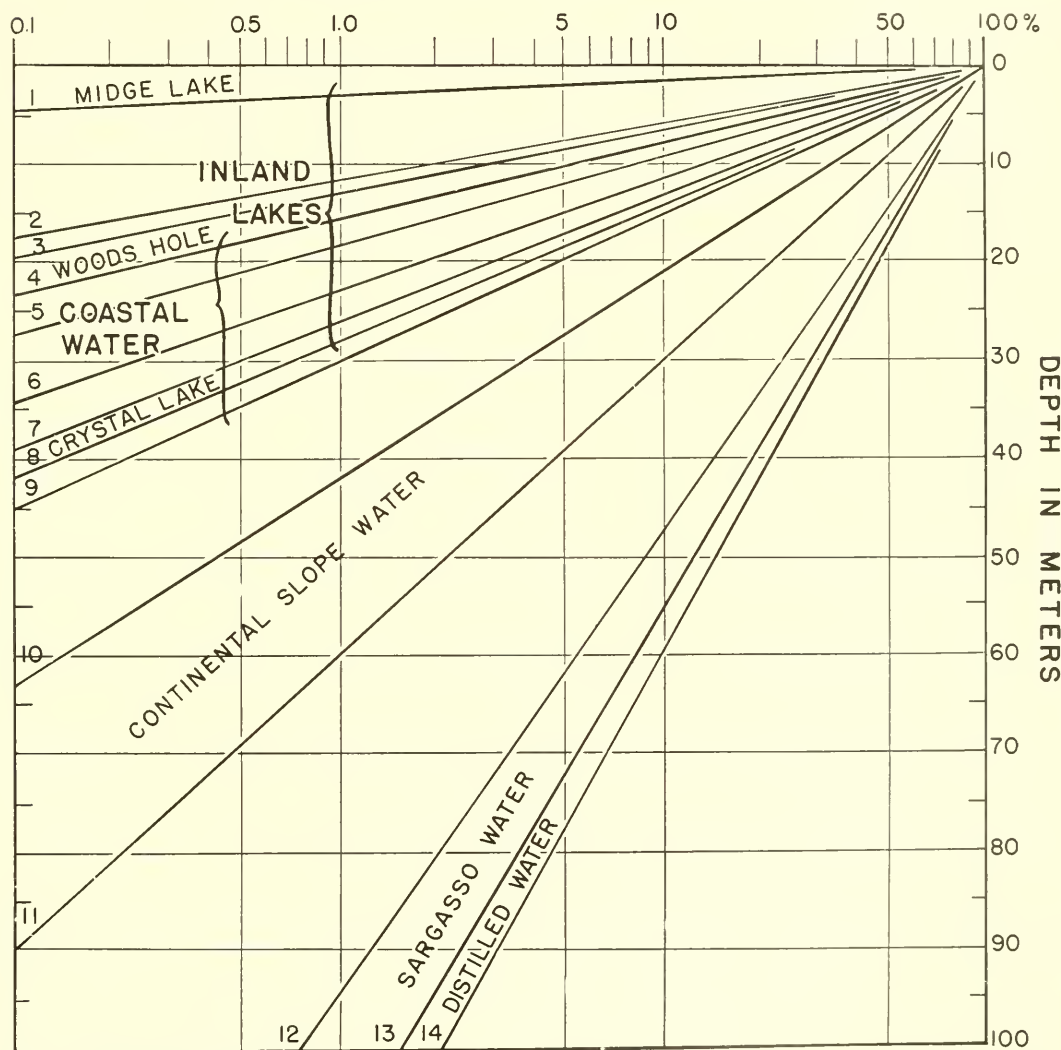


FIG. 3. Comparison of the rates of penetration of the yellow-green component of daylight into natural waters (Photometer sensitive to wave lengths 5000-6000Å). Curves show the relation between depth and illumination expressed as a percentage of the light at the surface. The curves represent the *average* value of the extinction coefficient for each series and no "surface loss" is included.

Curve	Location	Extinction coefficient (k)	Absorption per meter %	Authority
1	Midge Lake, Wisconsin	1.53	78	Birge and Juday (1930) Fig. 15
2	Trout Lake, Wisconsin	.40	33	" " " " Fig. 14
3	Gunflint Lake, Minnesota	.36	30	Erikson (1933) at 5450Å
4	Woods Hole Harbor	.30	26	Oster and Clarke (1935) Ser. 316
5	{ Thatcher Pass, San Juan Islands	.256	23	Utterback and Jorgenson (1934) at 5300Å
	Buzzards Bay	.25	22	Oster and Clarke (1935) Ser. 325
6	Vineyard Sound	.20	18	" " " " Ser. 322
7	Baltic Sea	.18	16	Pettersson and Landberg (1934) Fig. 2
8	Crystal Lake, Wisconsin	.16	15	Birge and Juday (1930) Fig. 14
9	English Channel	.155	14	Atkins and Poole (1933) Ser. 58
10	Gulf of Maine (deep basin)	.11	10	Oster and Clarke (1935) Ser. 301
11	{ Off Vancouver Island Continental Slope, s. of Nan- tucket Shoals	.079	7.6	Utterback and Jorgenson (1934) at 5300Å
	Gulf Stream	.074	7.2	Oster and Clarke (1935) Ser. 314
12		.049	5.0	" " " " Ser. 311
13	Cayman Sea (Caribbean)	.042	4.1	Clarke (1938b) Ser. 438
14	Distilled water	.039	3.8	James and Birge (1938) at 5460Å

material present have a *selective* action on light beyond that of the water itself, and the nature of the selective effect varies widely from one body of water to another. As a result it becomes necessary to measure separately the rate of penetration of each spectral region for each lake or oceanic area. Four typical cases are presented to illustrate the very great differences which are encountered in the selective action of natural waters.

In the Sargasso Sea (Fig. 4) the red part of the spectrum is absorbed at the most rapid rate, the yellow-green and violet components are reduced much more slowly, and the blue light penetrates the most effectively. The theoretical maximum for the transparency of any natural water is indicated in the figure by the distilled water curves for (1) the wavelength at which absorption is least ($4730\text{\AA}$, $k=0.005$) and (2) for the average of a band extending $500\text{\AA}$ each side of this (av. $k=0.010$). Sea water as transparent as the latter has actually been observed for limited strata in the Sargasso Sea (Clarke 1933). In Vineyard Sound (Fig. 5) the red component of sunlight is similarly absorbed more rapidly than any other, but here the yellow-green component is by far the most penetrating, and the blue and violet regions take an intermediate position. The same situation obtains in the clearest lakes as, for example,

in Crystal Lake. In Trout Lake, however, although the yellow-green component still penetrates the most effectively, blue light is absorbed a little more rapidly than the red (Fig. 5). In the case of a highly colored lake like Midge Lake the relative rates of absorption are just the reverse of those in very clear water, for here we find that red light is the most penetrating and blue the least with yellow in an intermediate position (Fig. 6).

The changes in the distribution of the solar energy at increasing depths which result from the differences in the selective action of the foregoing types of water are very pronounced. The situation in the Sargasso Sea is qualitatively similar to that which would occur in distilled water (Fig. 2). The energy distribution at various levels in Crystal Lake will serve as an example for the clearest inland waters or for most coastal waters (Fig. 7). Rudolph Lake has been taken as an illustration of a highly colored lake (Fig. 8). One observes that whereas in the clearest water blue light remains after the other parts of the spectrum have been removed, in the case of Crystal Lake the energy present at 15 meters consists almost entirely of yellow and green light, and in Rudolph Lake at 5 meters the energy is practically confined to the red and orange regions.

In the foregoing cases it has been

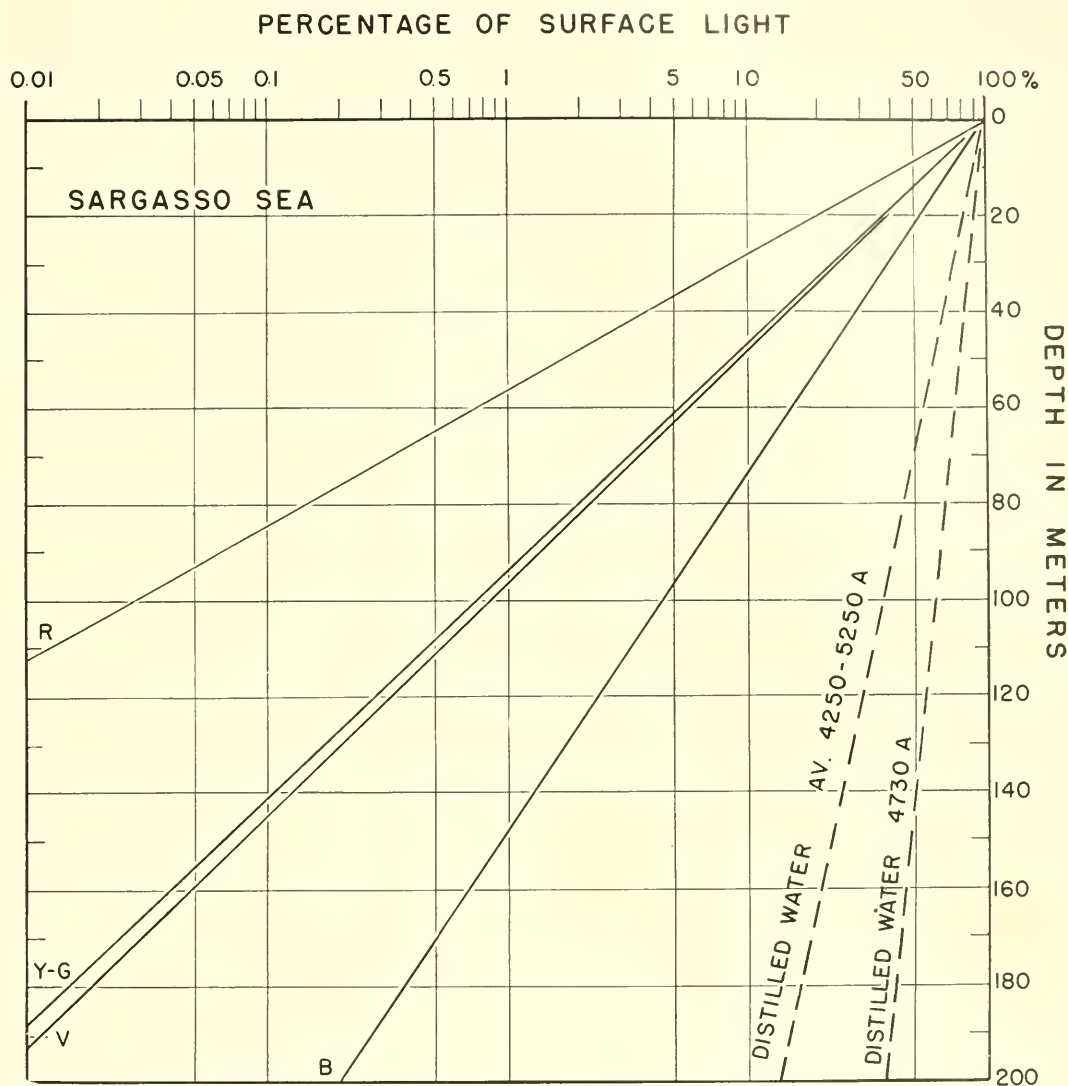


FIG. 4. Comparison of rates of penetration of four regions of the spectrum into the water of the Gulf Stream and Sargasso Sea. The curves represent the *average* values of the extinction coefficient as measured by Oster and Clarke (1935) and by Clarke (1933). The rate of penetration into distilled water for light at the wave length where absorption is least (4730Å, $k=0.005$) and for light extending 500Å each side of this (av. $k=0.010$) (from the data of James and Birge 1938).

assumed that the transparency of the water is uniform at all depths. This has often been found to be true especially where the water has been rendered quite homogeneous through effective mixing. In certain fjords and lakes, however, abrupt changes in transparency with depth have been reported (Pettersson 1934, Whitney 1938a). These indicate discrete layers of suspended material which may be of either organic or

inorganic origin, and which may have an important function as a "false bottom." The exact identification of the material constituting such strata presents an inviting problem.

The angular distribution of the light becomes altered after it enters the water not only because of refraction at the surface but also because of scattering within the water mass. The upward component was

found to be about 5 per cent of the downward component in coastal waters and about 2.5 per cent in the deep basin of the Gulf of Maine (Clarke 1936a). In the case of 16 Wisconsin lakes investigated by Whitney (1938b) this ratio ranged from 0.5 per cent to 4.8 per cent according to the lake. Within each lake, however, the light passing upwards remained a constant percentage of the downward light at all depths

that the total light from all directions reaching a point 5 to 10 meters below the surface was 1.5 times the illumination which would have been recorded by an ordinary plane horizontal photometer. However, a great deal more work is needed on this subject (cf. Johnson and Liljequist 1938).

The distribution in time of the illumination at any point is controlled by changes

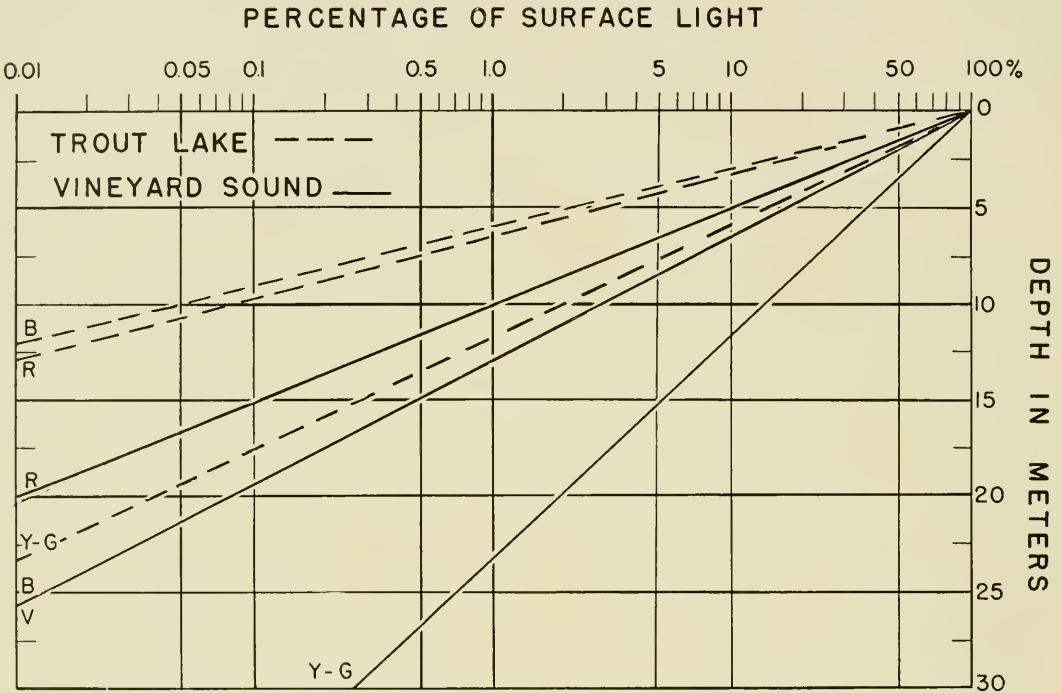


FIG. 5. Comparison of rates of penetration of four regions of the spectrum into Vineyard Sound (solid lines) and Trout Lake (broken lines). The curves represent the average values of the extinction coefficients as measured by Oster and Clarke (1935) for Vineyard Sound and by Birge and Juday (1930) for Trout Lake.

and the same is probably true of all oceanic areas. This finding agrees with the theoretical calculations of Whitney and is of great significance biologically because it means that the directional character of the light is not lost. Furthermore, since planktonic organisms can receive light from any direction we should have information not only on the amount of light passing vertically downward or upward but also on the radiation traversing the water at other angles. An attack on this problem has been begun by Pettersson (1938), who has found

in the length of day and by seasonal variation in transparency. The latter is of vital importance since it has been shown to be chiefly responsible for the tremendous differences in amount of light received daily by organisms at only moderate depths—as much as 10,000 × at 30 meters (Clarke 1938, 1939). The agents causing changes in transparency, however, are not adequately known and present another opportunity for research.

In dealing with the utilization of the light energy by aquatic animals and plants,

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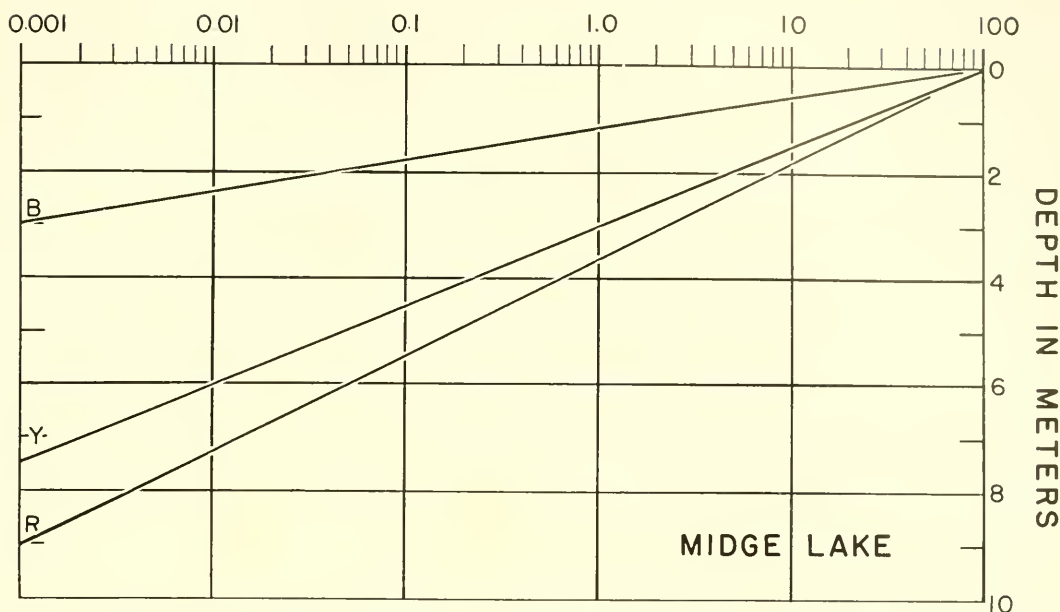


FIG. 6. Comparison of rates of penetration of three regions of the spectrum into Midge Lake. The curves represent *average* values of the extinction coefficients as measured by Birge and Juday (1930).

separate consideration will be given to the major subdivisions of the solar spectrum to which the following magnitudes may be roughly assigned: Infrared, 41 per cent; ultraviolet, 7 per cent; and visible, 52 per cent. As shown by Fig. 2, the infrared

radiation is almost entirely absorbed in the uppermost meter. The chief importance of the infrared is, therefore, the rapid heating of the surface stratum.

Ultraviolet light in large amounts is injurious to plankton and other organisms,

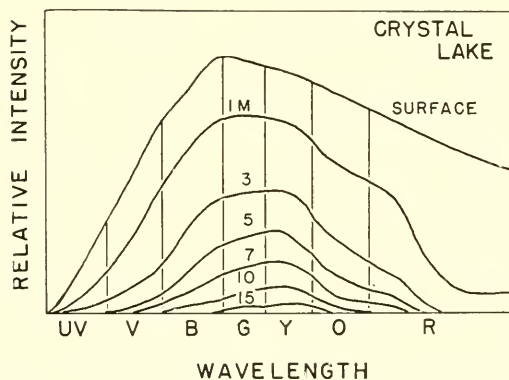


FIG. 7. Crystal Lake, Wisconsin. The spectral distribution of solar energy as it reaches the surface of the lake is given by the uppermost curve. The reduction in intensity and the changes in spectral distribution at successive depths in the lake are indicated by the curves beneath (from Birge and James 1939).

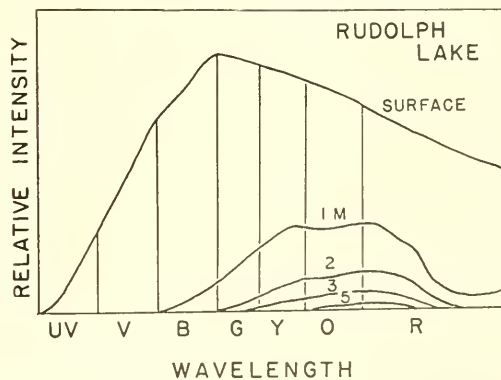


FIG. 8. Rudolph Lake, Wisconsin. The spectral distribution of solar energy as it reaches the lake's surface is given by the uppermost curve. The reduction in intensity and the changes in spectral distribution at successive depths in the lake are indicated by the curves beneath (from Birge and James 1939).

but according to ZoBell and McEwen (1935) virtually no bactericidal radiations penetrate sea water to as great a depth as 3

understood ways call for exact measurements of its rate of penetration. Yet serious disagreement exists on the rate of

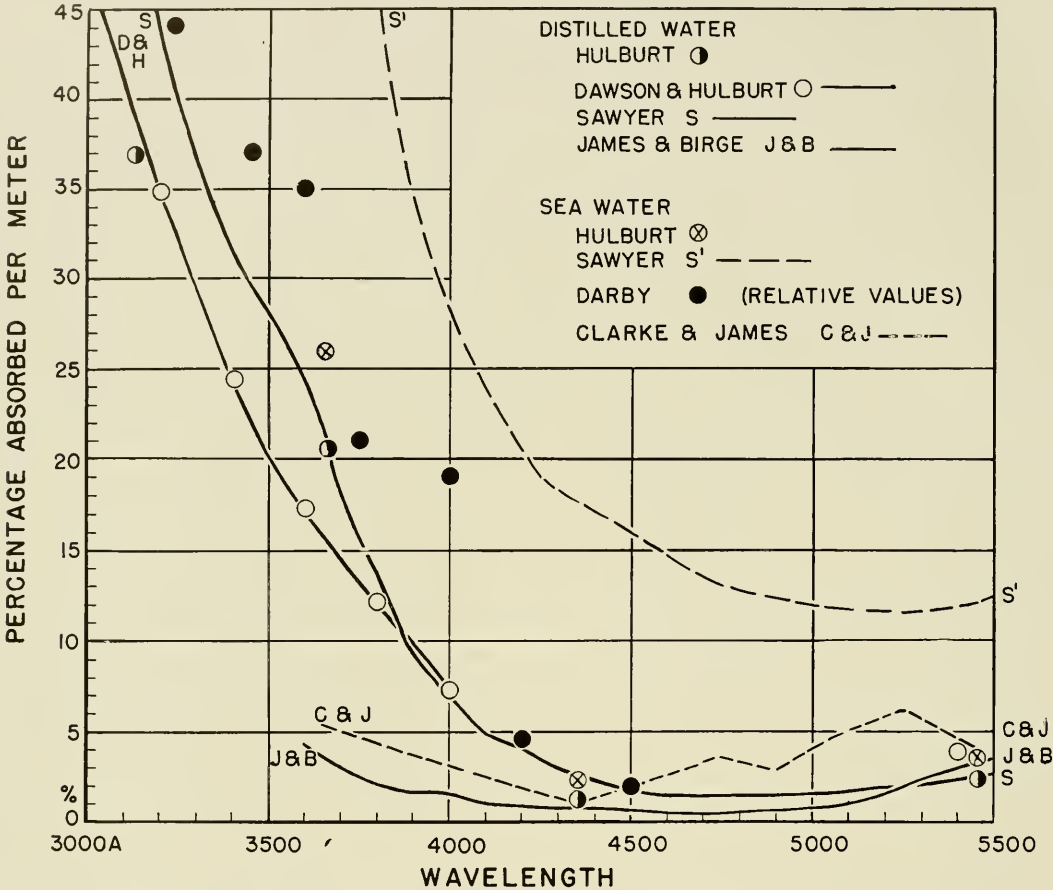


FIG. 9. Absorption of light by distilled water and by sea water at the ultraviolet end of the spectrum. Distilled water: Hulburt (1928); Dawson and Hulburt (1934); Sawyer (1931); and James and Birge (1938). Sea water: Hulburt (1928), from calculated values at 3130Å (87.8 per cent) and at 3660Å (25.9 per cent) and from data of Abbott, Fowle and Aldrich at 4360Å and at 5460Å (sea water from Caribbean agreed with these values); Sawyer (1931), laboratory measurement of water from Bay of Fundy off Head Harbor; Darby, Johnson, and Barnes (1937), relative values obtained at sea near Tortugas Laboratory, Gulf of Mexico; Clark and James (1939), laboratory measurement of water from Sargasso Sea after Berkefeld filtering.

meters. The beneficial effects of ultraviolet in vitamin formation* and in other poorly

absorption of ultraviolet light even for distilled water! In Fig. 9 the measurements of various workers at the short wavelength end of the spectrum are compared. Previously it had been supposed that ultraviolet was absorbed very rapidly by pure water itself, but the observations of James and Birge (1938) indicate a much lower absorption at least as far as 3600Å. It is essential to know whether this low rate

* Darby and Clarke (1937) report a relatively high concentration of vitamin D in *Sargassum* and they suggest that the vitamin finds its way into cod liver oil from this source through the connecting links of a food chain. The steps involved in this suggestion should be carefully worked out since it calls for a transfer through living agents of material from the very warm Sargasso water to the cold habitat of the cod.

continues to hold for the shorter, and more important, wavelengths or whether there is an abrupt upward turn. A similar disparity is to be found among the few measurements which have been made of natural waters (*cf.* Clarke and James 1939) due largely to the lack of a sensitive instrument suitable for field use. The exact determination of the rate of penetration of this important type of radiation is thus a matter which urgently needs attention.

Turning now to the visible component of the spectrum, we find that many observations exist on the degree of activity of fish and of plankton animals in relation to its intensity. The information obtained, however, has not yet been adequately applied to the ecological relationships of the species concerned. A prominent case in point is the diurnal migration of plankton. Although research in this field has shown conclusively that the daily change in illumination is primarily responsible for the migration, the internal physiological reactions which control direction and speed of swimming are poorly understood (Welsh 1938). Even less clear are the reasons why the vertical migration of one species differs from that of another and why the behavior of the same species varies profoundly from time to time and from place to place (Clarke 1934, Kikuchi 1938, and Johnson 1938). Nevertheless the stratification of 200 plankton, which results from these reactions to light, is an aid to the investigation of certain important problems such as the feeding of these animals and their role as food for fish.

According to a recent calculation (Clarke 1936b) sufficient illumination for vision in at least one species of fish exists at the bottom in those lakes and coastal oceanic areas whose transparencies have been measured. The minimum illumination required by other species should be similarly tested and the information applied to all types of natural waters. Since the spectral distribution of the light at only moderate depths differs so materially from that at the surface, careful testing of the spectral sensitivity of the various species is impera-

tive. The light receptors of some organisms must be exceedingly sensitive since Waterman, Nunnemacher, and Clarke (1939) have recently demonstrated a distinct diurnal migration of plankton at depths as great as 800 meters in the ocean. New information on the possibilities of vision for fish will have valuable applications to fisheries problems. It should be feasible to determine generally the depth and time of day when feeding requiring vision is possible, on the one hand, and when fish nets might be perceived and avoided on the other. The distance could be ascertained at which a submerged light is visible and its effect in attracting or repelling various types of fish.

The intensity of illumination controls photosynthesis and hence limits the depth of growth of both bottom-living and pelagic plants. For example, the lower limits for fixed plants in the following oceanic areas are:* in Baltic, 20 meters; off Iceland, 50 meters; and in Mediterranean, 130–160 meters. In lakes the lower limits are:† Trout Lake, 10–12 meters; Crystal Lake, 15–20 meters; and in Crater Lake, 12 meters. The maximum abundance of phytoplankton has been reported at the following depths:* off Syracuse, 50 meters; off California, 25–55 meters; and in north European waters, 10–30 meters. At these depths most of the radiant energy present is in the green or blue, but red light is most effective for photosynthesis (Manning 1938). Diatoms and other algae appear, however, to be able to use other parts of the visible spectrum effectively (Stanbury 1931). The mechanism which makes this possible requires elucidation.

The relative rates of photosynthesis at various levels beneath the surface have been investigated by measuring the oxygen evolved by phytoplankton placed in bottles and suspended at different depths. Near

* From Marshall and Orr (1928).

† From Juday (private communication). See also Juday (1934) and Hasler (1938). In lakes both fixed and planktonic plants have frequently been reported at depths far too great for photosynthesis. These plants must either be in a dormant or dying condition or else are living saprophytically (*cf.* Kozmiski 1938).

the surface the illumination has sometimes been found sufficiently strong to inhibit photosynthesis, although the exact explanation for this is wanting (Clarke 1936a and Riley 1938). Below the point of maximum photosynthesis the rate drops off to a depth at which no appreciable reaction takes place, but respiration continues at all levels to which living cells may be distributed. The intensity of light at which photosynthesis just balances respiration is termed the compensation intensity, the value of which has been reported in two recent investigations as 500 lux and 350 lux (or 0.3 per cent of noon sunlight) respectively (Pettersson, Höglund, and Landberg 1934, Pettersson 1938, and Jenkin 1937). Since the compensation intensity will naturally vary from species to species, further determinations for types important ecologically are seriously needed. The depth at which the compensation intensity is found, known as the compensation point, has been located (for short intervals) in a number of cases:* Sargasso Sea, greater than 100 meters; English Channel, 45 meters; Gulf of Maine, 24–30 meters; East Sound (W. coast of Canada), 10–19 meters; Trout Lake, Wis., 8–16 meters; Woods Hole Harbor, 7 meters. The depth of the compensation point over an average 24 hour period is, however, the significant value from the point of view of the continued growth and ecological role of each species. Marshall and Orr (1928), working in the Clyde Sea area, found that on this basis the depth varied from 2 meters to 30 meters according to the season. Further observations from this angle in other areas are obviously of the greatest importance. There appear to be no determinations of the compensation point for 24 hours for lakes!

The productivity of any body of water depends ultimately upon the efficiency with which the plants can transform radiant energy into the potential energy of organic tissue. Kozminski (1938) attempted to approach this problem by measuring directly the quantity and distribution of chloro-

phyll in lakes, but found that the measurements failed to give an exact index of the mass of the phytoplankton or of the intensity of photosynthesis because of the presence of inactive chlorophyll. He states, however, that "when it is possible to measure photosynthetically active chlorophyll only, this will be the best measure of productivity."

Another method of approach to this problem is the calculation of the quantity of carbohydrate produced on the basis of the amount of oxygen evolved by plant cells suspended in hanging bottles. Of the various experiments conducted by Manning *et al.* (1938) in Wisconsin lakes the highest quantum efficiency observed was .05. Since this value is so much lower than the value of .25 obtained by Warburg and Negelein (1923) in the laboratory, investigation of this discrepancy is demanded. Elsewhere Manning* has calculated on the basis of the average abundance of chlorophyll in a series of lakes that from 1.6 per cent to 14 per cent of the light incident on the lake is absorbed by the chloroplasts of the phytoplankton. An average value for the quantum efficiency under natural conditions according to Manning is .012 which is equivalent to an efficiency for photosynthesis of 2.7 per cent. When the two factors are taken together, we obtain:

Incident light absorbed			Efficiency of photosynthesis		Efficiency of production
min.	1.6%	×	2.7%	=	.043%
max.	14 "	×	2.7 "	=	.38 "

The efficiency with which aquatic algae manufacture carbohydrate is, therefore, only a small fraction of a per cent. And not all of this product would be found in the tissues of the plant because a large part of it is consumed concomitantly in respiration and other life processes.

It thus appears that most of the light

* "Photosynthesis in relation to light penetration into lake waters." Symposium of Hydrobiology. Joint meeting of the Limnological Society of America and the American Society of Zoologists, Indianapolis, Ind., December 30, 1937.

* From Pettersson, Höglund and Landberg (1934), Clarke (1936a), Jenkin (1937), and Manning, Juday and Wolf (1938).

incident on the surface of lakes or oceanic areas is absorbed by the water itself or by detritus and that only a very small part can be utilized by plants or animals. We conclude that aquatic organisms are existing under very unfavorable circumstances in regard to the utilization of solar energy. It is for this reason that the intensity, amount, and composition of the light are so frequently found to be limiting or highly significant factors in the aquatic environment. Attack on the unsolved problems outlined above is therefore urgent, and the extension of our present observations into other bodies of water and particularly over longer periods of time is of the greatest importance.

SUMMARY

The amount and nature of daylight in natural waters depends upon the surface loss, the selective absorption of the water itself, and the selective action of particulate and dissolved material. Further changes in the illumination result from differences in transparency with depth and with the season, differences in the length of day, and differences in the angular distribution of the light.

The biological significance of ultraviolet in natural waters is in doubt, but the visible component of light is important in the regulation of the activity of many animals, in the vision of fish, and especially in the photosynthesis of the plants. Since the utilization of light is very low even under the most favorable circumstances, it is understandable that light is so frequently a limiting factor in the aquatic environment.

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THE DISTRIBUTION OF BACTERIA IN LAKES

By ARTHUR T. HENRICI

DEPARTMENT OF BACTERIOLOGY AND IMMUNOLOGY, UNIVERSITY OF MINNESOTA,
MINNEAPOLIS, MINN.

Je mehr der Einblick in das Leben eines Sees vertieft werden soll, desto mehr müssen auch die Bakterien in den Bereich der Untersuchung gezogen werden; ja man darf sogar behaupten, dass für das Verständnis der oft stark ineinandergreifenden Lebenszyklen in einem See, besonders im eutrophen See, überhaupt für den gesamten Stoffhaushalt in einem stehenden Gewässer, die Kenntnis der Tätigkeit sowohl der im freien Wasser als der im Schlamm lebenden Bakterien unerlässlich ist.

—Huber-Pestalozzi (1938).

Thus quotation may well serve to indicate the nature of the problem to be solved in studying the bacteria of lakes. A similar quotation might be derived from a number of general works on limnology, for most limnologists have realized that bacteria play an important part in the economy of lakes. But definite information upon this phase of lake study is almost completely lacking; for bacteriology has lagged considerably behind the other biological sciences in participating in the study of lake ecology. Whereas botanists and zoologists have long since made their collections and classified their species, and have studied the distribution of them, so that they are now able to synthesize the results of their investigations from the standpoint of lake-types, etc., bacteriologists have yet to learn, for the most part, what species of bacteria live characteristically in water, and have only the most general ideas as to what they do there or how they are distributed. It is highly desirable that limnologists become more interested in bacteria, and bacteriologists more interested in limnology.

Our lack of knowledge of water bacteria is due largely to a lack of interest on the part of bacteriologists, who have been so concerned with the relations of bacteria to disease, agriculture, and industry that they have paid but little attention to bacteria of no "practical" importance. Most of the work on bacteria in water has been carried out either from the standpoint of potability

(the occurrence of disease-producing bacteria in the water) or from the standpoint of pollution (the self-purification of streams). Only a scattered few have done any work on the bacteria characteristic of the fresh water itself. The culture media used for the study of bacteria of medical importance are not suitable for the cultivation of the autochthonous water bacteria, and from the work of public health bacteriologists there developed an idea that there are no bacteria characteristic of water. The introduction of sodium caseinate (Nährstoff Heyden) medium by Düg-geli (1924) and by Fred. Wilson, and Davenport (1924), provided indications that there are true water bacteria, *i.e.*, species not derived from the surrounding soil or other pollution. During the past 15 years there has developed a slowly-growing literature on lake bacteria as such. This literature has been reviewed by Baier (1935). Only certain papers will be referred to here.

We incline toward the view that the main function of bacteria in lakes must be the decomposition of dead organic matter, leading to a mineralization of the elements composing this organic matter, so that these elements are again available to photosynthetic plants for the synthesis of new organic matter. Thus the lake bacteria link the ends of the food-chain, convert it into a cycle.

But this is not the only role of bacteria in lakes, and may not be the most important one. Our knowledge of bacteria in all habitats has been obtained through the use of artificial culture media, the composition of which (mainly organic) has been determined by habit established in studying bacteria of medical importance. Thus we know best the *heterotrophic* bacteria, those that obtain their energy by the oxidation

or fermentation of organic matter. By the use of purely inorganic media a number of bacterial species have been discovered which are not organisms of decay. These *autotrophic* bacteria are very probably also of great importance in the metabolism of lakes. They fall into two divisions: the chemosynthetic species which obtain energy from the oxidation of inorganic elements or compounds (hydrogen, sulphur, iron, ammonia, carbon monoxide), and the photosynthetic species. The latter, the red and green sulphur bacteria, possess pigments which, like chlorophyll, trap the energy of sunlight, and use it to transform carbon dioxide and hydrogen sulphide into organic matter. The chemosynthetic bacteria are extensively discussed by Waksman (*Principles of Soil Microbiology*, 1932); the photosynthetic bacteria, which are mainly aquatic in habitat, have been studied by van Niel (1931, 1935, and 1936) and van Niel and Muller (1931).

Heterotrophic bacteria must be listed as consuming organisms, autotrophic bacteria as producing organisms, in the economy of lakes. Both heterotrophic and autotrophic bacteria may of course serve as food for part of the zooplankton. The relative importance of bacteria as producing organisms in lakes has been discussed by Birge and Juday (1922), who concluded that they are relatively unimportant as compared with the higher phytoplankton. The degree to which bacteria may serve as food for the zooplankton has been discussed by Baier (1935) who cites further literature.

A consideration of the importance of bacteria as producers and consumers does not, however, adequately present the role of bacteria in the economy of lakes. Heterotrophic and autotrophic bacteria together are *transformers* of materials. Just as the essential character of protoplasm is its chemical instability, its power continuously to transform matter and energy, so from a biological standpoint the essential character of a lake is its ability continuously to transform matter and energy through the activities of its total fauna and flora. And in these transformations bacteria play a very large part, since they grow and trans-

form matter more rapidly than higher organisms, and because they can perform chemical reactions impossible to other organisms.

A few examples may serve to show the importance of bacteria in lake metabolism. Proteins derived from higher organisms are decomposed by heterotrophic bacteria, the nitrogen eventually liberated as ammonia; this ammonia is oxidized by autotrophic bacteria to nitrates. Under anaerobic conditions in the bottom muds, organic matter is fermented by heterotrophic bacteria that liberate methane and hydrogen; these gases are oxidized in the aerated waters above by autotrophic bacteria. Sulphates are reduced in the lake bottom by heterotrophic bacteria which are thus able to oxidize organic matter under anaerobic conditions; the resulting sulphides, diffusing to the aerated water above, are oxidized to sulphates by autotrophic bacteria. It is this complex interplay in the activities of different sorts of bacteria which is the most interesting and important part of a study of the role of bacteria in the economy of lakes.

These generalizations regarding the activities of lake bacteria are derived from our general knowledge of bacteria, not based upon extensive studies of the activities of bacteria in the lakes themselves. A proper study of lake bacteria should begin with an analytic and experimental study of the effects of various environmental factors upon individual species of water bacteria, to be followed by a synthetic study of the various lake environments, observing and correlating the natural occurrence of these factors and of the bacterial flora which they determine. We have as yet only a small amount of information regarding the characteristic species of water bacteria, we have not learned yet how to grow many of them in artificial cultures, so that we cannot even make a beginning of this study. All that we may state at the present time regarding the influence of environmental factors upon lake bacteria must be a generalization, again drawn from our knowledge of other kinds of bacteria.

We have seen that bacteria are very di-

verse in their food requirements. In this group nature has experimented with every possible mode of nutrition. It would be difficult to imagine a naturally-occurring environment that would not provide chemicals suitable for the growth of some sort of bacterium. They are equally versatile with regard to other environmental factors. There are bacteria known which can grow at temperatures below the freezing point; others that can grow at 80° C. There are bacteria that can grow in distilled water, others that can grow in damp salt. There are bacteria that can grow in acidities lower than pH 1, others in alkalinities as high as pH 13. There are bacteria that can grow in the complete absence of oxygen, others exposed to the air. From the standpoint of foodstuffs, temperatures, osmotic pressures, hydrogen-ion concentrations, oxidation-reduction potentials, bacteria are adapted to a wider range than any other group of living organisms, with the possible exception of the blue-green algae. One cannot imagine any sort of lake environment that would not provide a habitat for some sort of bacteria.

The problem of the relationship of bacteria to the productivity of lakes is very similar to the problem of their relationship to soil fertility. We have already developed an extensive soil bacteriology. The aquatic habitat differs from soil in two important particulars. Soil is normally well aerated; only when it is waterlogged is oxygenation reduced, and under such conditions the soil takes on the characters of an aquatic habitat. Lakes are often anaerobic for part of the year in their deeper portions, entirely so in their bottom deposits, where bacteria are most numerous. Thus anaerobic bacteria must be much more important in the ecology of lakes than in soil, and the decomposition of organic matter in lake bottoms must be very slow and imperfect as compared with that in the soil. A number of limnologists have recognized the importance of bacteria in the oxygen regimen of lakes; this topic has been extensively discussed by Grote (1934) and by Kusnetzow (1935). It is the tremendous oxygen-consuming power of the large num-

bers of bacteria in the lake bottom which makes for complete anaerobiosis a few millimeters below the mud-water interface, which causes oxygen to disappear below the thermocline in stratified eutrophic lakes, which causes fish to suffocate in shallow waters in the winter.

Secondly, soil differs from the aquatic habitat in that the latter is penetrated by light. We have as yet but little information on the effect of light on bacteria. It is well known that the ultraviolet portion of the spectrum is highly lethal, and it is widely believed that light is to a large extent responsible for the self-purification of polluted streams. Minder (1920) sought to explain the summer minimum of bacteria in Lake Zürich, and the low counts obtained from surface samples, on the basis of lethal action of sunlight. This view was also supported by Buchner (1893) and by Zih (1932). This belief is, however, not adequately supported by experimental evidence; there is confusion regarding the degree to which the lethal ultraviolet light rays penetrate into water.

The work of Snow and Fred (1926) confirmed by a number of other later workers has shown that pigmented bacteria, relatively rare in soil, are abundant in lake waters. From 30 per cent to 50 per cent of the colonies appearing in plate cultures are pigmented. This peculiarity of the lake flora is shared by the sea and by streams, and is probably related to the fact that light can penetrate into the aquatic habitat. Chromogenic bacteria are almost completely absent in the dark waters of dystrophic lakes. They are found on the leaves of plants, and it is noteworthy that the only pigmented parasitic bacteria of man occur most abundantly on the skin. Pigment production by bacteria appears to be clearly correlated with exposure to light, but we do not know what function the pigments perform.

In earlier literature on water bacteriology one finds the question raised as to whether there is a characteristic autochthonous bacterial flora of water. This question was usually answered in the negative. But all of the earlier work was car-

ried out almost exclusively from a sanitary standpoint, and the culture media used were not suitable for the growth of characteristic water bacteria. Seeing on their plates only the same sorts of colonies that grew on plates exposed to the air or inoculated with dust or soil, they came to the conclusion that bacteria in the water had merely been brought there from the surrounding land. It is true that some of the early microscopists described and illustrated a number of bacteria from water that are morphologically distinctive, and obviously characteristic of the water. But teachers and textbooks of bacteriology have almost always dismissed these with the simple statement that they cannot be cultivated in artificial media and are therefore not important. They have usually been referred to rather vaguely as "higher" bacteria, outside the scope of true bacteriology.

Huber-Pestalozzi (1938) has divided the water bacteria into two groups—the morphologically identifiable and those which can only be identified by physiological characters. The latter, of course, must be grown in pure cultures for their final identification. The morphologically identifiable species, many of which have been described and illustrated by Huber-Pestalozzi, are very unusual to those acquainted only with the cocci, bacilli, and spirilla of medical bacteriology. They fall in three orders: the filamentous ensheathed Chlamydo-bacteriales, the sulphur bacteria or Thiobacteriales, and the recently discovered Caulobacteriales (Henrici and Johnson 1935). The latter grow in the water on stalks similar to some diatoms and protozoa. Some of the morphologically identifiable water bacteria deposit iron in their sheaths or on their stalks, or as capsules, in a characteristic manner, which helps in their recognition. The iron bacteria have recently been monographed by Dorff (1934). The Thiobacteriales have been described by Bavendamm (1924).

The species of water bacteria which require cultivation for their identification have not been extensively studied. Aside from the dominance of chromogenic species, we have no clear evidence of an autochthon-

ous flora of Eubacteriales in lakes. But it is the author's opinion that this lack of evidence is due merely to lack of investigation. There is some scattered evidence that when sufficient pure culture studies have been made they will eventually show a true aquatic flora of bacteria. Thus, Klayver and van Reenen (1933) have shown that in water *Azotobacter agilis* is the important nitrogen-fixing bacterium, not the *Azotobacter chroocoeum* commonly found in soil. The genus *Spirillum* has long been known as dominantly aquatic; it has been studied but little until recently Giesberger (1936) contributed substantially to our knowledge of both the physiology and taxonomy of the genus.

I cannot too strongly emphasize our almost complete lack of knowledge of the taxonomy of water bacteria. Only a few scattered groups have received any attention at all. To illustrate, the fourth edition of Bergey's *Manual of Determinative Bacteriology* lists but 27 species of the genus *Corynebacterium*, practically all of them parasitic in animals. I have found that about 15 per cent of all the bacteria which may be cultivated from the bottom deposits of lakes fall in this genus. They belong to an unknown number of species, none of which has as yet been described. We may make but little progress in the study of bacteria in relation to lake ecology until bacteriologists become sufficiently interested to work out the taxonomy of the common lake bacteria.

A lack of knowledge of the species of water bacteria need not, however, entirely impede studies of bacteria in relation to the household of lakes. We may learn considerable about the productivity of lakes, about the distribution of life in the lakes, by simple quantitative determinations of the plankton, without subjecting these to taxonomic analysis. Similarly we may study the distribution of the total bacterial flora in different types of lakes, in different parts of lakes, and at different seasons, and so gain some idea as to their activities without determining the species. Indeed such general surveys are desirable before extensive taxonomic studies are

undertaken, since they will furnish a guide as to where and when to make collections. It should be kept in mind, however, that such purely quantitative studies furnish only an imperfect and incomplete picture of the lake bacteria. For instance, there are more periphytic bacteria active in the bottom meter of Lake Mendota in the winter, the temperature 4°C , than at any other level at any season. These must be a particular group of cold-loving bacteria that find optimum conditions at the bottom of the lake when it is frozen. What species, we do not know.

The quantitative distribution of bacteria in lakes has been studied by the use of four distinct techniques. The one most commonly used is the method used in all branches of bacteriology, that of plate counting. A sample of water, properly diluted, is mixed with melted nutrient agar, poured into a Petri dish, incubated, and the number of colonies counted. This method has a serious disadvantage in that no single medium will allow the growth of all the cultivable bacteria, and some of the water bacteria will not grow in any medium. For the most part, only organic media have been used, and only heterotrophic bacteria have been cultivated. Earlier studies were conducted primarily from the standpoint of sanitation, and the medium used, standard beef infusion agar, was more suitable for the cultivation of parasitic bacteria. Such studies have not yielded results that are significant from the standpoint of hydrobiology. With the introduction of media more suitable for work on lake bacteria, particularly the dilute sodium caseinate-glucose medium of Fred and his associates, more significant results were obtained.

I have used a medium similar to that mentioned, but modified to include a wider variety of organic materials. It is composed of sodium caseinate, peptone, glycerol, starch, and dibasic potassium phosphate, 0.05 per cent of each in tap water, with 1.5 per cent agar. This dilute medium has given higher counts than the caseinate-glucose medium. I began my work on lake bacteria with a prejudice against the plate

count. As I have found the results of such counts to correlate with the results of microscopic counts and with other data, I have been forced to revise my opinion. The plate count method may be developed into a very useful one with further study.

Plate cultures must be prepared as soon as possible after the sample has been collected, since not only the total number but also the relative proportions of different kinds of bacteria will alter markedly if the sample is stored. To be accurate, plate counts must be made in replicates of at least five for each dilution. The preparation of plates requires large amounts of glassware and other equipment not easily provided in a field laboratory. This has been perhaps one of the most important factors in limiting the study of lake bacteria. The author has found that plating under field conditions can be greatly simplified by the use of flat-sided bottles instead of the customary Petri dishes. Lotion bottles of 120 cc capacity fitted with screw caps are used. The agar medium is placed in these bottles in 30 cc amounts in the home laboratory, where they are sterilized. In the field the agar can be melted by placing the bottles in a pan of boiling water.

The published literature on plate counts of lake bacteria from a hydrobiological standpoint has been extensively reviewed by Baier (1935).

The distribution of lake bacteria may be further studied by the use of selective media. Thus one may prepare a solution containing no source of nitrogen. In such a medium only those bacteria which can use atmospheric nitrogen may grow. Merely inoculating a tube of this medium with some lake water will show whether nitrogen-fixing bacteria are present or absent. By preparing a series of dilutions of the water, and inoculating a number of replicate tubes from each dilution, one may estimate the numbers of bacteria belonging to a particular physiological group in the sample. By the use of a variety of selective media, all sorts of physiological groups may be determined.

Selective media were used by Domogalla, Fred, and Peterson (1926) to study the

occurrence of nitrifying and denitrifying bacteria in Lake Mendota; by Klein and Steiner (1929) to determine the occurrence of urea-splitting, nitrogen-fixing, nitrifying, denitrifying, sulphur-oxidizing, and sulphate-reducing bacteria in the lower Lake Lunz; by Steiner (1931) to determine the occurrence of cellulose- and chitin-decomposing bacteria in the same lake; by Williams and McCoy (1935) to determine the occurrence of a variety of physiological groups in the bottom deposit of Lake Mendota; and by Baier (1935) to determine the occurrence of nitrifying, denitrifying, nitrogen-fixing, cellulose- and urea-decomposing bacteria in several ponds near Kiel. None of these studies have been sufficiently extensive or quantitative to warrant any generalizations regarding the distribution of various physiologic groups. They have served, however, to indicate that all of the important physiologic groups found in soil are also found in lakes.

Nearly all of the investigators who have used culture methods to study bacteria from the standpoint of limnology have collected their samples with one or another modification of the apparatus introduced by Russell (1892). Test-tubes are drawn out to a capillary, partially evacuated, and sealed. They are clamped in a holder attached to a line, lowered to the desired depth, and a messenger is dropped which breaks the capillary and allows the sample to be sucked into the tube. Such an apparatus useful in studying lakes has been described and illustrated by Wilson (1920).

Culture methods are the only ones so far developed which are suitable for the study of bottom muds. Because bottom deposits contain much larger numbers of bacteria than do the lake waters, bottom samples must be more highly diluted for quantitative studies; otherwise cultures are made by the same techniques as for water. Henrici and McCoy (1938) have discussed and described equipment for collecting bottom samples for bacteriological analysis.

Since cultural methods require elaborate apparatus and large amounts of glassware not readily available in field laboratories, and especially because no single medium

will permit of a growth of more than a fraction of the species of bacteria, it is natural that attempts toward a more direct study of the water bacteria should be made. Except for highly polluted waters, the bacteria occur in numbers too small to permit a direct microscopic enumeration or observation; they must first be concentrated. Snow and Fred (1926) attempted to do this by centrifuging after adding aluminum hydroxide as a flocculating agent. Cholodny (1929) filtered the water samples through collodion membranes, examining smears of the sediment which collected on the filter. Kusnetzow and Karsinkin (1931) evaporated water samples under diminished pressure at 35° to 40° C. The results of various studies based upon these methods have been reviewed by Bere (1933) who used the method of Kusnetzow and Karsinkin on a study of various Wisconsin lakes.

Such a method includes in the count both living and dead bacteria, and does not distinguish between bacteria washed into the lake from the surrounding land and those active in the water. All of these methods require considerable manipulation which may introduce errors. With evaporated samples, the occurrence of particles of precipitated mineral matter may obscure the field, especially in the case of hard waters. In all cases particles of debris hardly distinguishable from bacteria may occur. The figures published by Kusnetzow and Karsinkin, millions per cubic centimeter, are much too high for an unpolluted lake; such quantities of bacteria would make the water obviously turbid. These methods have all served to show that bacteria are more numerous in the water than plate counts would indicate, the microscopic counts running from 8 to 4,000 times as high as the plate counts. They have not, however, provided data which permit of generalizations regarding the distribution of lake bacteria.

A fourth method for studying lake bacteria was introduced by Naumann (1925) for the study of the morphology of certain water bacteria, and adapted independently by myself (Henrici 1933), and by Kar-

sinkin (1934) for quantitative studies of the distribution of lake bacteria. The method consists in submerging microscope slides in the lake for a time. Bacteria attach themselves to the glass and grow there. The slides are removed, dried, fixed, stained, and examined under the microscope. The bacteria may be readily counted, and morphologically distinctive species may be determined separately.

Such a method has great advantages over the others. It takes into account only those bacteria which are actually growing in the water, ignoring those that are dead or which have merely been washed into the lake from the surrounding land. It brings into the picture the large numbers of morphologically peculiar water bacteria which have not been so far cultivated in the laboratory. It requires no elaborate apparatus, and is therefore well adapted to field use.

I have described elsewhere (Henrici 1936) the use of this method as a quantitative procedure and have discussed its accuracy. Briefly, it has been found that fairly reliable results may be obtained if counts are made from two pairs of 50×75 mm slides suspended at each station, one pair to be removed after a short period of immersion, the second after a longer period. The duration of exposure must be roughly adjusted to the productivity of the station, which may be readily determined after a little experience. The bacteria are counted in each of 50 fields on each of the four slides, the counts for each slide are converted to numbers of bacteria per square millimeter per day of immersion, and the results from the four slides are averaged.

The microscopic counts of bacteria growing on submerged slides is limited in accuracy due to the highly varied distribution of the bacteria on the slides. Irregularity of distribution is greater with low counts. With very high counts errors arise due to the difficulty in distinguishing all of the cells; such counts are likely to be too low because cells have been overlooked. Separate counts which show small differences should be scrutinized from a statistical standpoint before conclusions are drawn.

Where a number of observations from the same habitat are averaged, the results of course are more accurate in proportion to the number of observations. In the data to be presented in the following pages, standard deviations are not presented though they have been calculated and are on file. In general it may be stated that a mere doubling of numbers in individual observations is not likely to be significant, that a five-fold difference is almost certainly significant. It is my impression that counts of bacteria from submerged slides have a degree of useful accuracy greater than is indicated by statistical analyses based upon the distribution of the bacteria on the individual slides. Thus the curve shown in Fig. 3 is regular and agrees well with the other curves, even though in some instances the differences between two successive observations are not statistically significant.

The submerged slide method has a disadvantage in that it collects only those bacteria which can grow attached to submerged surfaces. There is, however, growing evidence that this is a characteristic of a large portion of the water bacteria. I have found that in a broad way there is a good correlation between the results from submerged slides and from plate counts, although in individual observations such a correlation may be lacking. If large numbers of observations at various stations are studied, there is found a fairly close correlation between the two sets of counts; for 100 pairs of counts the coefficient of correlation was found to be 0.625.

ZoBell and Allen (1933) found that 24 of 73 strains of marine bacteria isolated in pure cultures were capable of attaching themselves to and growing upon submerged slides in the laboratory. Hotchkiss and Waksman (1936) noted a correlation between counts of bacteria on submerged slides, and plate counts, in laboratory experiments with sea water; constants could be determined from experimental data which permitted the calculation of the numbers to be expected from the slide counts, if the plate counts are known. Kusnetzow (1937) submerged slides for a short time and then made cultures of the

bacteria growing on the glass. A comparison of these with cultures isolated directly from the water showed that different species were obtained by the two methods. All of the pure cultures isolated directly from the water were capable of growing upon submerged slides in the laboratory.

The submerged slide method offers another approach to the study of lake bacteria. The distribution of morphologically identifiable but non-cultivable species may be followed through different habitats. From a correlation of the distribution with physical and chemical characters of the habitats, one may surmise something regarding the physiological requirements of the organism, and proceed to devise a suitable culture medium. The iron bacterium, *Siderocapsa major*, is readily recognizable. Searching for this organism on slides submerged in a variety of lakes shows that it occurs only in hard-water drainage lakes neutral or alkaline in reaction. Since ferrous iron is insoluble in alkaline water, this organism must deposit iron by utilizing organic iron compounds. Presumably the organism could be grown in a medium with organic iron, slightly alkaline in reaction, though this has not been tried yet (Hardman and Henriei 1939).

Bacteria occur in all of the ecologic groups of aquatic life recognized by the limnologist. Some of our earliest descriptions of bacteria concern material obtained from the "wasserspiegel," the iridescent film of neuston organisms which collects upon the surface of still waters. Bacterial pellicles develop, however, only upon small shallow bodies of water high in organic matter, and are not a factor in lakes. The bacteria suspended or swimming in the water, and which grow in plate cultures or appear in microscopic examinations of concentrated lake water are to be included in the plankton. Both microscopic and cultural studies of bottom deposits show that the benthic bacteria are vastly greater in numbers than anywhere in the water above. Probably, however, bacteria are more characteristically a part of the periphyton than of any other ecologic group. This term, introduced by Behning (1928) and not yet

in general use by limnologists, is the equivalent of what the Germans call "aufwuchsorganismen," and refers to those aquatic organisms which grow attached to submerged surfaces. There is much evidence that the bacteria in the water are not, for the most part, free-floating, but are attached to algae or other plankton organisms. There is evidence that the great abundance of bacteria in bottom deposits is due largely to the fact that they are carried to the bottom by the sedimentation of larger organisms. Rocks and rooted plants, piles and piers, the bottoms of boats, all submerged surfaces soon become coated with a film of periphytic bacteria. It is quite possible that the few bacteria free in the water are but motile reproductive bodies, swimmers, derived from attached periphytic bacteria, just as one may trap in the plankton motile spores of sessile algae.

ZoBell and Anderson (1936) have shown that the growth of bacteria in stored water samples is probably due mainly to the influence of the surface of the vessel in which the water is stored. That is, an inert surface like glass is sufficient to cause an increase in the bacteria. They showed that this increase is roughly proportional to the amount of surface introduced into the environment. This effect is probably due to the concentration of organic matter adsorbed onto the surface. While the total amount of dissolved matter in the water may be sufficient to support a larger population of bacteria, the concentration is too low to permit of their fullest development; when the concentration is increased by adsorption the bacteria grow further. That such a concentration of organic matter from the water on submerged surfaces actually occurs has been demonstrated by Stark, Stadler, and McCoy (1938). It is clear, therefore, that the occurrence of surfaces either as a support for the bacteria, or in concentrating their food elements, is a factor of fundamental importance in the growth of aquatic bacteria.

In the preceding paragraphs I have presented a rather condensed resumé of the status of lake bacteriology from the standpoint of hydrobiology. The papers cited do

not constitute an exhaustive bibliography, but many of them carry bibliographies from which further references may be derived. In the following pages I propose to present mainly the results of my own investigations which have been carried on through four seasons on eleven lakes of Minnesota and Wisconsin. For the most part the data are derived from microscopic counts of periphytic bacteria deposited upon submerged slides, over 3,000 of which have been counted; but numerous plate counts of both water samples and bottom deposits were also made.

The work was begun at Lake Alexander in central Minnesota where observations

Pike, pike-perch, perch, sunfish, and black bass are abundant. No chemical analyses are available, but the water is obviously very hard and alkaline in reaction. *Chara* is an abundant bottom plant and lime-encrusted *Potamogetons* are common. The map shown in Fig. 1 indicates the hydrography of the portion of the lake where observations were made and also shows the location of stations at which samples were taken.

Through the kindness of the Wisconsin Geological and Natural History Survey further data were collected during the summer of 1935 from nine lakes in northeastern Wisconsin, viz., Brazelle, Boulder, Crystal,

TABLE I

VERTICAL AND HORIZONTAL DISTRIBUTION OF PERIPHYTIC BACTERIA, LAKE ALEXANDER.
NUMBERS OF BACTERIA PER SQUARE MM PER DAY DEPOSITED UPON SUBMERGED
SLIDES. MEDIAN DATE OF IMMERSION, AUG. 7, 1934.

Depth, meters	Stations												
	A	B	C	D	E	F	G	H	I	J	K	L	M
0	512	660	286	637		980	2634	304	718	846	758	255	631
1	559	631	380			3230	3353	849	1310	960	2129	611	1305
2		524	404	694	1299	486	455	1359	416	143	303	274	275
3			1083	652	693	161	275	172	185	297	142	137	537
4				1520	554	469	200	85	376	213	223	247	218
5					785	115	232	325	150	411	101	147	154
6						951	299	120	197	153	114	552	179
7							2355	633	108	28	231	169	155
8								55	45	364	149	363	51
9									27	44	159	254	210
10										26	160	425	682
11											16	1601	576
12												51	107
13													36

were made through the summers of 1933 and 1934. This is a shallow, unstratified hard-water lake of glacial origin. It receives drainage from several small brooks which are dry most of the year, and discharges into the Mississippi drainage. During the period of these studies there was very little rainfall. The lake level was below the level of the outlet, and the lake was temporarily a seepage lake. It has, however, all of the general characters of a drainage lake. It is highly productive. The shallow protected bays are choked with plant life. The lake "blooms" in the summer.

Helmet, Little John, Mary, Muskellunge, Trout, and Weber lakes. The hydrographic, physical, and chemical characteristics of these lakes have been thoroughly studied and the data are available in numerous publications of the Wisconsin Geological and Natural History Survey (see Juday and Birge 1930, 1931, 1933; Juday, Birge, and Meloche 1935, 1938; and other papers). Again through the kindness of the Wisconsin group further observations were made on Lake Mendota during the summer of 1936. The characteristics of Lake Mendota are available in numerous publications.

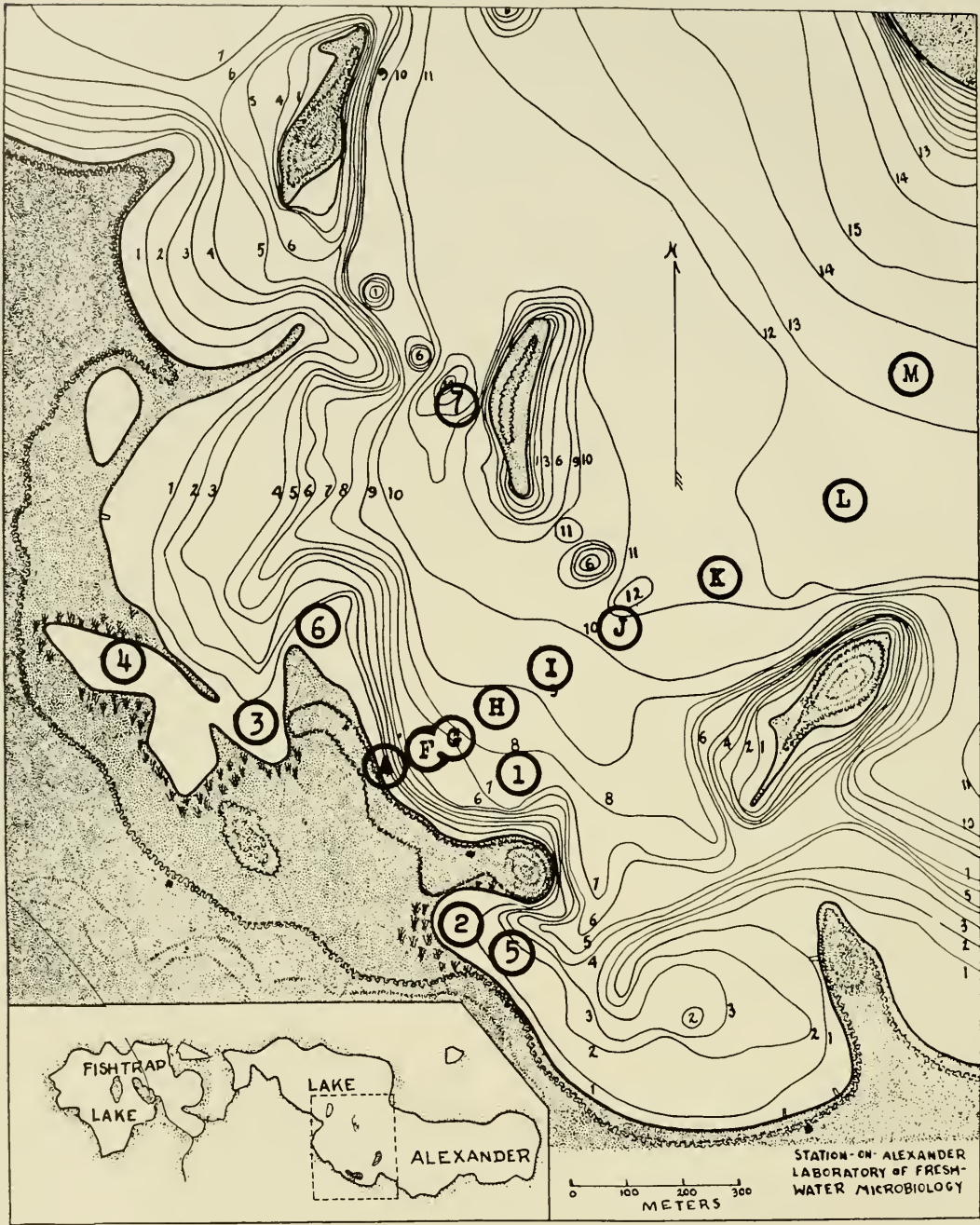


FIG. 1.

Fig. 2 shows the location of stations where observations were made.

VERTICAL DISTRIBUTION OF BACTERIA

Most studies of lake bacteria based upon culture methods have failed to show any

significant variations in the vertical distribution. Thus Kleiber (1894) failed to observe any differences in numbers of bacteria at different levels in Lake Zürich. Pfenniger (1902), working on the same lake, found during summer stagnation that bac-

teria were fewer at the surface, more numerous at 100 meters depth than at 30 meters. These results were confirmed by Minder (1920). Dügge (1924) noted that bacteria showed a definite stratification in

TABLE II

VERTICAL AND HORIZONTAL DISTRIBUTION OF PERI-PHYTIC BACTERIA, LAKE MENDOTA.
NUMBERS OF BACTERIA PER SQUARE MM PER DAY ON SLIDES. MEDIAN DATE OF IMMERSION, JULY 20, 1936.

Depth, meters	Stations			
	4	3	2	1
0	1718	471	590	241
3		422	337	434
6			373	126
9			493	465
12				413
15				229
18				223

sharply separated. Bacteria growing on caseinate agar were numerous in the upper layers, absent in the lower ones. The latter contained sulphate-reducing bacteria, while red sulphur bacteria were abundant at the border between the two layers. Klein and Steiner (1929), working on lower Lake Lunz, found cultivable bacteria to be somewhat more numerous at the surface and near the bottom than at other levels. Fred, Wilson, and Davenport (1924) found only slight and variable differences in the vertical distribution of bacteria in Lake Mendota. Graham and Young (1934) did not find any very striking variations in the vertical distribution of bacteria in Flathead Lake; there was a slight tendency toward greater numbers at the very surface and smaller numbers near the bottom.

Kusnetzow (1925), using plate cultures, found no marked differences in the vertical



FIG. 2.

the peculiar Lake Ritom in Switzerland. This lake exhibits an upper portion of normal water, and a lower portion high in salt and H_2S content. These two portions are

distribution in Lake Glubokoje, in Russia; but Kusnetzow and Karsinkin (1931), using their microscopic method of counting, observed a remarkable increase (up to 6,000.-

000 per cc) in the thermocline of the same lake, associated with an oxygen-minimum in that zone. Bere (1933) using the microscopic method of Kusnetzow and Karsinkin, observed differences in the vertical distribution of bacteria in various lakes of north-eastern Wisconsin. Bacteria were found to be most numerous in the upper 5 meters of Trout Lake, the numbers being uniformly less below that level. Crystal Lake and Silver Lake showed no definite variations. Mary Lake and Nebish Lake showed a distinct progressive increase with depth.

Nearly all of the studies which have been mentioned were carried out during the summer months in stratified lakes. There is no clear trend apparent. In some instances higher counts at the surface may be due to the influence of inflowing water as was suggested by Pfenniger. Except for the peculiar lake studied by Duggeli, there is no sharp differentiation between the epilimnion and hypolimnion. The author has previously published data (Henrici 1936) comparing plate counts and counts of periphytic bacteria at various levels in four lakes. It was found that in some cases the periphytic bacteria showed marked differ-

ences while plate counts showed none. This may be explained by the fact that the plate count represents not only active, but also dormant bacteria. Undoubtedly bacteria are constantly settling from the upper layers to lower ones, although in the latter they may be unable to grow because of temperature, or oxygen, or other relations. The slide counts indicate only bacteria growing in the water.

Karsinkin (1934) studied the distribution of periphytic bacteria in Lake Glubokoje. The results varied somewhat with the season and with the duration of exposure of the slides. Observations were made at the beginning of September when the lake was still stratified. More bacteria were found in the epilimnion than in the hypolimnion; there were two maxima, one near the surface and one at the thermocline. Observations made at the end of September, when the lake had turned over, showed greatly reduced numbers which were uniform from top to bottom.

In Tables III, IV, and V there are presented data on the vertical distribution of periphytic bacteria in eight of the lakes which I have studied. Data have been se-

TABLE III
VERTICAL DISTRIBUTION OF PERIPHYTIC BACTERIA DURING MIDSUMMER STRATIFICATION.
EUTROPHIC LAKES.

Lake Alexander			Lake Mendota			Big Muskellunge Lake		
Depth, meters	Temp., Aug. 22	Bacteria* Aug. 10†	Depth, meters	Temp., Aug. 10	Bacteria* Aug. 10†	Depth, meters	July 23 Temp.,	Bacteria* July 23†
0	25°	Too many	0	25.0°	422	0	26.1°	343
2		724	3	24.4°	549	2		517
3		1152	6	24.0°	240	4	24.6°	603
4		230	9	22.4°	346	6		232
5		140	12	17.8°	180	8	15.5°	117
6		318	15	14.2°	430	10		Too few
7		506	18	12.0°	126	12	10.4°	53
8		668				14		91
9		610				16	8.6°	89
10		504				19	8.5°	12
11		235						
12		119						
13		266						
14	21°	33						

* Bacteria per square mm per day deposited upon slides.
† Median date of period of immersion.

TABLE IV
VERTICAL DISTRIBUTION OF PERIPHYTIC BACTERIA DURING MIDSUMMER STRATIFICATION,
OLIGOTROPHIC LAKES,
1935

Trout Lake			Crystal Lake			Weber Lake		
Depth, meters	Temp., Aug. 27	Bacteria* Aug. 14†	Depth, meters	Temp., Aug. 4	Bacteria* Aug. 4†	Depth, meters	Temp., Aug. 4	Bacteria* Aug. 4†
0	20.3°	927	0	24.0°	93	0	25.0°	86
2	20.3°	554	2	24.0°	59	2	23.7°	77
4		376	4	22.7°	22	4	23.4°	112
6		439	6	22.5°	230	6	23.1°	164
8		448	8	18.6°	48	8	17.8°	245
10	19.5°	42	10	15.8°	57	10	14.0°	371
12	12.7°	60	12	13.2°	45			
14	11.3°	62	14	12.3°	50			
16	8.9°	67	16	11.6°	42			
18	8.3°	257						
20	7.5°	903						
22	7.3°	65						
25	6.7°	63						
28	6.5°	57						
31	6.3°	34						

* Bacteria per square mm per day deposited upon slides.

† Median date of period of immersion.

lected from the various observations to coincide as far as possible with regard to season, choosing those observations which were made near August 1. Since the time of immersion of the slides has been varied according to the productivity of the lakes, the time-coincidence is only approximate.

Lake Alexander is not thermally stratified. The temperature difference noted in the table is the greatest that has been observed. It will be noted that bacteria were too numerous to count at the very surface, though the heavy coating of the slides was due perhaps more to algae than to bacteria.

TABLE V
VERTICAL DISTRIBUTION OF PERIPHYTIC BACTERIA DURING MIDSUMMER STRATIFICATION,
DYSTROPHIC LAKES,
1935

Mary Lake			Helmet Lake		
Depth, meters	Temp., July 10	Bacteria* July 25†	Depth, meters	Temp., July 25	Bacteria* July 23†
0	25.0°	324	0	25.0°	3060
2	13.5°	54	2	16.5°	99
4	5.3°	Too few	4	9.1°	95
6	4.1°	" "	6	6.6°	Too few
8	4.0°	" "	8	6.4°	" "
10	4.0°	" "	10	6.3°	" "
12	4.0°	" "			
14	4.0°	" "			
16	4.0°	" "			
19	4.3°	" "			

* Bacteria per square mm per day deposited upon slides.

† Median date of period of immersion.

But the counts are distinctly higher in the top 3 meters. This has been observed repeatedly in this lake at several stations during midsummer, not in other lakes which I have studied. It is correlated with the enormous production of blue-green algae. The lake regularly blooms in August, and the floating plankton is largely concentrated at the surface. Below the 3 meter level, there are no striking or consistent variations until the very bottom is reached, where there is a decrease that has also been noted in other observations in this lake.

Lake Mendota is stratified, the thermocline lying at about 12 meters depth. While counts from the epilimnion average higher than those from the hypolimnion, the difference is slight and probably not significant. More significant differences are found in Muskellunge Lake, where the thermocline occurs at 8 meters depth; below this level the counts are much less than those in the upper layers. There is also a much sharper difference in temperature between the epilimnion and the hypolimnion than in Lake Mendota.

A similar distribution of bacteria is found in Trout Lake, the deepest that has been studied. Here the periphytic bacteria are much less numerous below the thermocline, and there is a correspondingly great difference in temperatures. Crystal Lake, which is shallower and with less sharp stratification, shows an almost uniform distribution from top to bottom, while Weber Lake, still shallower, shows a progressive increase toward the bottom.

The two dystrophic lakes, Mary and Helmet, show striking vertical distributions of the periphytic bacteria. In both of these the thermocline is at the surface; the temperature drops very rapidly. Periphytic bacteria are relatively abundant at the surface, almost completely absent in the lower levels; even after four weeks of immersion they were too few to count.

From the data presented it seems evident that periphytic bacteria show a marked decrease below the thermocline in those lakes which are sharply stratified (Glubokoje, Muskellunge, Trout, Mary, and Helmet)

while they are fairly uniform in distribution in shallower or less sharply stratified lakes (Alexander, Mendota, Crystal, and Weber). The vertical variations are probably due almost entirely to temperature; they have been observed in eutrophic, oligotrophic, and dystrophic types, and are more marked with greater temperature differences.

In the data presented there are several anomalous counts recorded. Thus in Muskellunge Lake, although consistent results were obtained at other levels, the slides at 10 meters were almost blank; in Trout Lake, unusually high figures were obtained at 18 and 20 meters, although at all other levels in the hypolimnion the counts were low; an anomalous high count is noted at 6 meters in Crystal Lake. Such local anomalous counts have been noted in other observations. They are of such a magnitude that they must be statistically significant, but I am at a loss to explain them. They may be due to the same causes which give rise to local variations in turbidity, discovered and described by Whitney (1938) and designated by him "microstratification." It is noteworthy that Whitney found local increases in turbidity to be associated with increases in organic matter and bacteria (plate counts).

Bacteria are more numerous in the bottom deposits of lakes than in the water. From data published by Henrici and McCoy (1938) it can be computed that the average bacteria per cubic centimeter in bottom deposits was from 12 to 680 times as great as the number per cubic centimeter in the water; these figures are based upon plate counts from nine different lakes. The greater number of bacteria in the bottom is probably due to several different factors, the most important being the tendency of the bacteria to be adsorbed by or otherwise attached to solid particles in the water, and to be carried by these particles to the bottom. Kleiber (1894) noted that large numbers of bacteria brought into Lake Zürich by inflowing streams extended only a short distance into the lake, and attributed their disappearance to sedimentation, and this

observation has been repeated by several other later writers. Rubentschik, Roisin, and Bieljansky (1936) found that lake bacteria (especially those cultivated from bottom deposits), could be adsorbed from aqueous suspensions by bottom ooze from lakes.

The distribution of bacteria in bottom deposits can be determined only by plate cultures. Bacteria are not deposited upon slides in numbers at all commensurate with their abundance in the mud, and because of the large amount of debris, direct microscopic counts are impossible. Henrici and McCoy (1938) have reviewed the published literature on the distribution of bacteria in bottom deposits. They found that bacteria are most abundant at the mud-water interface. They decrease with depth in a rather irregular manner with different samples, but this irregularity is due to accidental variations or to technical errors. When numbers of samples are averaged, the bacteria are found to decrease with depth in a regular manner; the numbers plotted against depth in the bottom form a logarithmic curve. The rate of decrease is therefore constant.

The larger numbers of bacteria in the bottom deposit, determined entirely by plate counts, do not necessarily indicate that their activities are greater than in the water above. Since the bottom is usually very cold, and anaerobic, it is quite possible that the bacteria there are relatively inactive. The concentration of organic matter is, of course, much greater in the bottom deposit than in the water; but this is the less readily decomposed organic matter, since presumably the more readily decomposed material will be made soluble shortly after the death of aquatic organisms, i.e., before or immediately after they have sunk to the bottom. The logarithmic curve of decrease of bacteria in the bottom has been compared by Henrici and McCoy to the logarithmic death curve in disinfection experiments; they suggest that it may indicate that bacteria are active only at the very surface of the bottom, dying below. A consideration of these facts will indicate that we are as yet unable to compare the relative impor-

tance of bacteria in the water and in the bottom deposit from the standpoint of their activities.

Summary of Vertical Distribution. Bacteria may be more numerous at the surface of the water in some lakes; this is probably due to the accumulation of floating plankton at the surface, and is most apparent in lakes that bloom. Plate counts do not show marked differences between the epilimnion and hypolimnion, but such differences are noted in counts of bacteria on submerged slides, in the case of sharply stratified lakes; they are probably due to temperature differences. There is only slight evidence that bacteria increase in the thermocline. They may show sharp local variations in vertical distribution associated with microstratification. Bacteria are more abundant in the bottom deposit than in the water, and most abundant at the mud-water interface, decreasing at a constant rate below this level. Their abundance in the bottom is probably due mainly to sedimentation.

HORIZONTAL DISTRIBUTION OF BACTERIA

Very little previous work has been published on the horizontal distribution of bacteria in lakes. Pfenniger (1902) found the bacteria to be uniformly distributed in the surface waters at various stations in Lake Zürich. Klein and Steiner (1929) found somewhat higher plate counts from surface water samples taken near the banks than in the open water of lower Lake Lunz.

I have collected considerable data on the horizontal distribution of bacteria in Lake Alexander. Both plate counts and counts of periphytic bacteria on submerged slides are available. During the summer of 1933 collections were made at seven stations, those marked with numbers on the map (Fig. 1). During the summer of 1934 collections were made at the stations marked with letters on the map, to provide a sort of bacteriological transect of the lake.

Stations 1 and 7 are open-lake stations. Station 2 is in a sheltered bay, at the very edge of the water, where a dense mat of *Ceratophyllum*, *Najas*, *Elodea*, and various *Potamogetons* merge with a marsh of cat-

tails and sedges. Station 3 is a similar littoral station, but somewhat different in character. Here the bottom is carpeted with *Chara*, and wild rice is the dominant emergent plant. The bottom here is almost pure marl. Station 4 is a shallow sheltered lagoon so choked with aquatic plants (pond lilies, *Potamogetons*, *Elodea*, *Myriophyllum*, etc.) that a boat is pushed through with difficulty. Station 5 was chosen as transitional between the sheltered littoral stations and the open lake. Here the water is about 2 meters deep. The bottom is covered by *Ceratophyllum*, but there are no emergent plants. Station 6 was chosen as an exposed littoral station. Here the bottom is made of boulders covered with *Cladophora* and *Rivularia*.

TABLE VI
HORIZONTAL DISTRIBUTION OF BACTERIA IN LAKE
ALEXANDER.

Station	Periphytic bacteria*	Plate counts, water†	Plate counts, bottom deposit‡
Station 1 ...	247	928	93,450
Station 2 ...	2725	8701	278,600
Station 3 ...	1387	10224	126,100,000
Station 4 ...	3279	28554	150,050,000
Station 5 ...	395	3190	1,103,400
Station 6 ...	662	1927	
Station 7 ...		901	79,900

* Bacteria per square mm per day deposited upon submerged slides.
† Bacteria per cc of surface water.
‡ Bacteria per cc of bottom deposit, from surface of bottom.

Table VI shows the results of counts of bacteria from these seven stations. In most of the shallow water stations slides were submerged only at the surface. For comparison, therefore, only surface data from the other stations are presented, and the results of plate counts are also based only on surface samples. The table presents the averages of a number of observations made from May to October, inclusive.

A study of this table shows, first, a fairly close parallelism between the three sets of data; the shoreward distribution of bacteria in the water, or in the mud, or growing upon

submerged surfaces, appears to be affected in the same way. It will be noted that the three protected littoral stations with abundant aquatic plants show very high counts, especially of periphytic bacteria. The exposed littoral station (6) shows counts only slightly higher than the open water stations. The transitional station (5) resembles the open lake as regards the periphytic bacteria, but is similar to the sheltered bays as regards the plate counts.

Probably the most important factor determining the shoreward distribution of the bacteria is the occurrence of aquatic plants. Where these are abundant, bacteria are numerous. Mere shallowness of the water is not an important factor. It is probable that the increase of bacteria in the vicinity of larger aquatic plants is due to larger amounts of dissolved organic matter in the water, derived from these plants. And it is probable that the surface provided by these plants is also a factor. The marked increase in the bacteria of the bottom deposit in the sheltered littoral stations is also due to the larger amount of organic matter provided by the rooted plants. The bottom deposit in these stations is a coarse, fibrous material made up largely of plant remains.

Table I shows the results of the transect made in 1934. The shore at Station A is a wave-swept sandy beach. Beginning at a depth of about one meter, there occur some rooted plants which increase in size and abundance with increased depth. These are mainly *Potamogetons*, but towards deeper water there occurs an extensive bed of *Ceratophyllum*. This probably extends to a depth of 6 or 7 meters.

Stations were established at each one meter contour line, and slides were fastened at each meter of depth. The results are a little irregular, but certain tendencies are apparent. The bacteria were deposited on the slides in larger numbers at or near the surface throughout the deeper part of the lake. This is again to be attributed to the occurrence of floating blue-green algae. The lake was blooming during the period of observation. Further, the bacteria are more abundant on the slides suspended in the

weed bed, particularly at the bottom. Beyond the weed bed the numbers are smaller at the bottom.

Again it is seen that the occurrence of plants affects markedly the distribution of the periphytic bacteria; both the floating plankton and the rooted plants near shore exert an influence. A comparison of the data presented in Table I with those shown in Table II will emphasize this influence of the plant life upon the bacteria. Table II shows the results of a similar but less extensive transect of Lake Mendota carried out in 1936. The locations of the stations are shown on the map (Fig. 2). The shore here is also a wave-swept sandy beach. There are no rooted plants in the zone studied, nor was the lake blooming. The periphytic bacteria are quite uniformly distributed, save for an increase at the very shore.

It has been noted that in Lake Alexander the numbers of bacteria in the bottom deposit are much greater in the sheltered littoral stations than in the open lake. Klein and Steiner (1929) found somewhat smaller numbers in the littoral stations at lower Lake Lunz. The stations were on an exposed shore, but rooted plants were present. Henrici and McCoy (1938) found a rather marked decrease in the bottom bacteria of Lake Mendota as the shore is approached. Samples were taken from the stations indi-

deposit, the bacteria decrease in numbers. The decrease of both humus and bacteria in the bottom deposit in these observations is to be attributed to wave action.

Summary of Horizontal Distribution. The shoreward distribution of bacteria is profoundly affected by the occurrence of rooted aquatic plants. In sheltered bays periphytic bacteria, bottom bacteria, and bacteria cultivated on agar plates are much more abundant than in the open lake. Even on an exposed shore periphytic bacteria are somewhat more numerous if there is a weed bed in the deeper water near shore. Bacteria in the bottom deposit decrease in numbers from profundal to littoral stations where there are no aquatic plants and the bottom becomes sandy toward shore.

SEASONAL DISTRIBUTION OF BACTERIA

Only a small amount of published investigations of lake bacteria has been sufficiently extensive or continuous to furnish information on seasonal variations. In particular, winter observations are lacking.

Pfenniger (1902) observed a summer minimum, with spring and autumn maxima, in Lake Zürich. This was confirmed by Minder (1920) who attributed the decrease during the summer to the action of sunlight. A summer minimum was noted also by Ruttner (1932) at Lake Lunz, and by Graham (1934) in Flathead Lake. Zih (1932) noted, in addition, a winter minimum at Lake Lunz. Pfenniger believed that the death of plankton organisms in the autumn was responsible for an increase of the bacteria at that time. Ruttner suggested that the semiannual turnover of the lakes was responsible for the spring and autumn maxima, but noted also that the highest counts coincided with the period of melting snows. Graham considered the melting snows of spring and the rains of autumn to be responsible for increases of bacteria, the bacteria being washed into the lake from the surrounding land. It will be noted that these observations were all made on high mountain lakes, presumably oligotrophic in type.

Fred, Wilson, and Davenport (1924) con-

TABLE VII

SHOREWARD DISTRIBUTION OF BOTTOM BACTERIA,
LAKE MENDOTA.

		Depth, meters	Bacteria per cc*
Station	A	20	753,500
"	5	20	836,900
"	1	18	249,580
"	2	9	38,180
"	3	5	40,700
"	4	1	35,650

* Averages of counts at all levels to 18 cm.

cated in Fig. 2, and the results are summarized in Table VII. Here the shore is sandy, and as the amount of black humus-like material becomes less abundant in the bottom

ducted extensive observations over three years on Lake Mendota. The results varied from year to year; there was a summer maximum in 1920, an autumn maximum in 1921, and a spring maximum in 1922. They discuss the complexity of factors which may influence seasonal variations in the plate counts, and emphasized the importance of rainfall; the counts were apparently influenced markedly by the washing of bacteria into the lake from the drainage basin.

The investigations of Domogalla, Fred, and Peterson (1926) have provided some in-

Sulphate reduction occurred only during the winter and early spring.

The author has previously published (Henrici 1937) a report on seasonal fluctuations of bacteria in Lake Alexander. The essential data are shown in Fig. 3, reproduced from that paper. The curves show the numbers of bacteria in plate counts, periphytic bacteria, and the volume of net plankton. Samples were collected at Station 1 (Fig. 1). The reader is referred to the original paper for details of technique.

Lake Alexander is unstratified, therefore

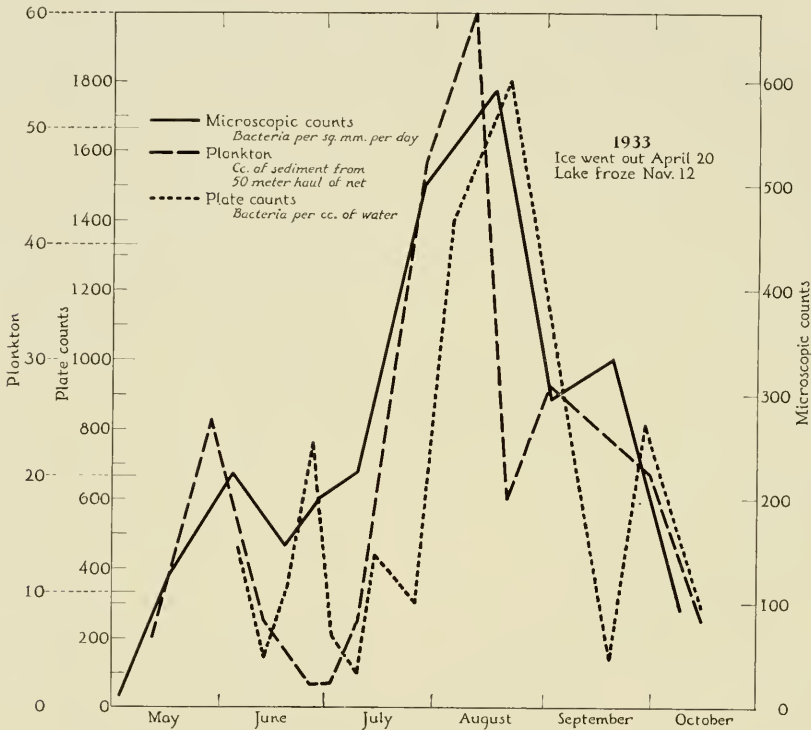


FIG. 3.

formation on seasonal variations in the activities of bacteria concerned in the nitrogen cycle. They found that nitrification was most intense during the late summer and autumn, when ammonia and organic nitrogen reached the highest concentrations; while nitrate reduction was least during the summer. Klein and Steiner (1929) found reverse conditions at Lake Lunz. Nitrification was most active in the winter, at which season denitrification was reduced to zero.

free from the effects of turnover. The observations were made during a drought year when the lake was singularly free from surface drainage. The lake is highly productive and blooms in the summer, in this respect quite different from the high mountain lakes mentioned previously.

It will be seen that the plankton pulses were an important factor in determining the occurrence of seasonal variations of the bacteria. Both sets of counts of bacteria

follow closely the curve for total plankton, but with a lag which is greater in the case of the plate counts. There were three plankton pulses—a spring and autumn growth of diatoms and a midsummer growth of blue-green algae. There are also three peaks to the curves for bacteria.

It was previously noted that periphytic bacteria were more numerous on slides suspended in the upper layers of Lake Alexander during the period of blooming, *i.e.*, August. The data presented in Fig. 3 were all collected from the surface. Table VIII shows both vertical and seasonal variations

fluctuations of the periphytic bacteria in Lake Mendota. It was previously noted that the summer stratification of this lake is not sufficiently sharp to affect obviously the vertical distribution of the bacteria. Under the ice in winter the bacteria are uniformly few in number until the bottom meter is reached, where they show an amazing increase. Noted in three successive observations, this must be significant. After the ice went out and the lake warmed up, the bacteria increased in number and became rather uniformly distributed from top to bottom.

TABLE VIII
DISTRIBUTION OF PERIPHYTIC BACTERIA BY DEPTH AND SEASON, LAKE ALEXANDER.*
NUMBERS OF BACTERIA PER SQ. MM PER DAY DEPOSITED UPON SUBMERGED SLIDES.
DATES ARE MEDIAN DATES OF PERIOD OF IMMERSION.
1933

Depth, meters	Apr. 30	May 18	Jun. 6	Jun. 20	Jun. 30	Jul. 9	Jul. 29	Aug. 17	Sep. 3	Sep. 21	Oct. 7
0	20.9	124.6	222.7	157.6	204.4	226.7		881.2	290.0		96.2
1	32.9	109.1		118.5	271.2	237.3		1075.2	313.9		117.6
2	21.3	132.3		201.6	318.8	251.6		954.3	319.6	329.2	213.2
3	36.6	52.0		262.3	358.3	329.3		343.6	366.5	332.2	211.7
4	19.1	91.8	432.8	227.3	456.0	171.5		683.1	303.8	529.2	124.3
5	15.7	168.4	369.1	328.2	295.7	237.7	205.3	761.6	590.3	1160.1	134.2
6	20.9	168.2	759.0	516.0	671.7	171.6	265.9	516.4	371.1	212.7	328.2
7	29.7	32.4		278.9	412.5	373.7	367.0	1194.8	505.2		129.9

* All observations at Station 1.

at Station 1. It will be seen that, although there are some anomalous counts, the vertical distribution remains fairly uniform throughout the year, except during August when distinctly higher counts occur at the surface. It will be noted that at all levels the counts are lower during early spring and late autumn, when the temperature was lower.

Table IX shows seasonal fluctuations of the periphytic bacteria at the various littoral stations in Lake Alexander. It is found that the bacteria do not fluctuate with the seasons so extensively as do those in the open water station. There is, however, a tendency for the bacteria to be decreased in numbers as the water cools in the autumn.

Table X shows both vertical and seasonal

We have as yet no adequate data on seasonal fluctuations of bacteria in the bottom deposits. Williams and McCoy (1935) noted only minor differences in samples from Lake Mendota taken during the winter and during the summer. Karsinkin and Kusnetzow (1931), using a modification of Winogradsky's method for the direct microscopic examination of soil, found that the bacteria in the bottom deposit increased progressively from May to September. The author considers this method entirely unreliable as a quantitative procedure. Speranskaja (1935) found that the bottom deposits of the Russian lakes increased in their content of nitrogen, sugar, hemicelluloses, and cellulose in the autumn, and that these substances decreased during winter stagnation. Kusnetzow and Kusnetzowa (1935) consid-

TABLE IX
SEASONAL VARIATIONS OF PERIPHYTIC BACTERIA, SURFACE WATER, LITTORAL STATIONS
OF LAKE ALEXANDER.

1933 Date	Station 2		Station 3		Station 4		Station 5		Station 6	
	Temp.	Bact.	Temp.	Bact.	Temp.	Bact.	Temp.	Bact.	Temp.	Bact.
5- 6		1291								
5-17	21	1041	17	1522	17	3583				
5-25			18	1515			15	200		
6- 3			20	585	19	1980	20	209		
6-11			26	2028	26	2009	27	149		
6-19			28	5738		2836		350		
6-26			30	650	30	4464	30	517		
7- 1			31	1888	31	9454				
7- 2							31	543		
7- 3									30	527
7- 7									32	1211
7- 8	27	4394	31	1211	31	3066	28	930		
7-15			30	833	30	3545				
7-16									31	377
7-17							28	510		
7-19									30	1125
7-24			30	2087	30	2094	30	443	30	350
7-26	26	5302								
8-15							23	602		
8-17	26	2251			26	2801				
8-18			26	880						
8-19									25	591
8-24	22	1384	23	484	22	3377				
8-28							28	451		
8-30					22	2857			23	543
8-31	25	3130								
9- 1			22	392						
9- 7	25	3836	25	690						
9-12							25	177		
9-15					26	1130				
9-25					16	2572				
10- 4							15	76		
10-15				242						
10-26	12	1897								

Temperatures are means of readings at beginning and end of immersion. Dates are median dates.

ered the accumulation of these substances in the bottom deposit to be important in determining the production of methane, and Kusnetzow (1935) believed that the absence of oxygen in "fish-suffocating" lakes under winter conditions is due to the liberation of hydrogen and methane from the bottom deposits of such lakes. Rossolimo and Kusnetzowa (1934) found methane-producing bacteria to be more abundant in the bottom deposits in winter than in summer. Perhaps these facts have some bearing upon the large numbers of periphytic bacteria

noted at the bottom of Lake Mendota in winter.
Summary of Seasonal Distribution. Seasonal fluctuations of bacteria apparently are different in different types of lakes. In high mountain lakes the semi-annual turnover, distributing bottom bacteria through the water, apparently determines the maxima, though the effect of spring thaws and autumn rains may be a factor. Plate counts are probably affected considerably by surface drainage washing bacteria into the lakes. In a highly eutrophic lake the plank-

TABLE X
DISTRIBUTION OF PERIPHYTIC BACTERIA BY DEPTH AND SEASON, LAKE MENDOTA.*
NUMBERS OF BACTERIA PER SQ. MM PER DAY DEPOSITED UPON SUBMERGED SLIDES.
DATES ARE MEDIAN DATES OF PERIOD OF IMMERSION.
1936

Depth, meters	Jan. 16	Feb. 20	Mar. 1	May 4	Jun. 28	Jul. 1	Jul. 20	Aug. 10	Sept. 19
0		44.1	13.3	354.7	179.0	1211.5	241.1	422.2	494.7
3	15.1	32.1	73.1	43.8	642.6	537.1	433.5	549.1	122.6
6	28.1	72.8	29.8	12.6	248.8	115.1	126.4	240.3	174.6
9	20.3	55.8	14.7	60.6	384.5	347.0	464.6	345.6	454.7
15	48.9	9.8	66.5		337.7	149.2	412.9	179.7	302.6
12	16.7	15.5	168.7	134.5	492.5	203.3	228.7	429.9	70.1
18	2010.2	1560.8	937.2	149.1	412.9	887.7	223.4	125.6	

* Observations from Jan. 16 to May 4 at Station A; from June 28 to Sept. 19 at Station 1.

ton pulses appeared to determine seasonal variations of the bacteria. The activities of periphytic bacteria vary with the temperature, but this is more apparent in open water stations than littoral ones. Periphytic bacteria were found to be unusually abundant in the bottom meter of Mendota during winter stagnation. There are no adequate data on seasonal variations of bacteria in the bottom deposits.

ABUNDANCE OF BACTERIA IN DIFFERENT TYPES OF LAKES

In spite of numerous exceptions, the classification of lakes into three basic types—eutrophic, oligotrophic and dystrophic—has remained a useful concept. It is now quite clear that dystrophic lakes are a class apart, but that eutrophic and oligotrophic lakes tend to form a graded series, quite distinct at the extremes, but with intermediate types often difficult to classify. Of the various characteristics used to distinguish eutrophic from oligotrophic lakes, the disappearance of oxygen in the hypolimnion of the former during summer stagnation is probably the most important. The decrease of oxygen has been attributed to several agents. Alsterberg (1927) thought it was due to the oxygen-consuming capacity of the bacteria growing in the sedimented organic matter of the bottom deposit. This has been perhaps the most widely accepted explanation. Kusnetzow and Karsinkin (1931) believed that the respiration of bac-

teria in the water of the hypolimnion itself was responsible for the decrease of oxygen. This opinion was based largely on the results of their studies of the enormous numbers of bacteria found by direct microscopic counting of evaporated samples from Lake Beloje and Lake Glubokoje. I have already expressed scepticism regarding the accuracy of the method. If the figures are correct, the numbers of bacteria in these lakes must be much larger than those usually encountered in unpolluted waters. Later Kusnetzow (1935) suggested that the decrease of oxygen in the hypolimnion was due in part to the displacement of oxygen by hydrogen and methane liberated from the bottom deposit through the activities of anaerobic bacteria, in part to the oxidation of these gases by autotrophic bacteria in the water. It is quite possible that all of these agencies combine to consume oxygen. In any case, it appears to be the activities of the bacteria in the lower parts of the lake which are concerned. The subdivision of lakes on the basis of the oxygen content of their hypolimnions is, in fact, a sort of measurement of the organic matter which can be oxidized by bacteria, similar to the measurement of the "biological oxygen demand" used by sewage bacteriologists.

Dystrophic lakes differ from the eutrophic-oligotrophic series in many respects, but from a bacteriological standpoint the most important is the large quantity of peculiar organic matter in the water, oc-

curring mostly as colloidal material, and its deposition in the bottom. There is much evidence that this material is not easily decomposed by bacteria, that it is quite different from the organic matter deposited in eutrophic lakes. Indeed, there is a suggestion that it is slightly antiseptic. Further characteristics of such lakes, important from a bacteriological standpoint, are the sharp stratification with the thermocline at or near the surface; the often strongly acid

numbers and kinds of bacteria characteristic of each type.

Table XI presents a summary of available data on the relative numbers of bacteria in eleven lakes, grouped according to types. It is not pretended that these data are adequate for any final conclusions; many more lakes will have to be studied, and more observations will need to be made on each lake. The data may serve, however, to indicate roughly what may be expected from further

TABLE XI
COMPARISON OF NUMBERS OF BACTERIA IN DIFFERENT LAKES.

Lakes	Periphytic bacteria ¹	Plate counts, water ²	Plate counts, bottom deposit ³	Microscopic counts, water ⁴
Brazelle lake	3,853	2,963	44,600	2,000,000
Eutrophic lakes				
Boulder	711		47,000	98,000
Alexander	526	675	144,240	
Little John	402	505	39,050	64,500
Mendota	375		609,300	975,000
Muskellunge	197	133	10,930	400,000
Mean	442	438	170,100	384,400
Oligotrophic lakes				
Weber	183	132	2,350	45,000
Trout	177	66	29,790	85,500
Crystal	63	80	2,160	36,000
Mean	141	93	11,400	55,500
Dystrophic lakes				
Helmet	377	380	120,300	394,000
Mary	24	58	39,450	745,500
Mean	200	219	79,880	569,750

¹ Bacteria per square mm per day deposited upon slides.
² Colonies per cc of water on agar plates.
³ Bacteria per cc of bottom mud on agar plates. (From Henriei and McCoy, 1938.)
⁴ Bacteria per cc of water computed from counts of evaporated samples. (From Bere, 1933.)

reaction, and the failure of light to penetrate through the deeply colored water. These facts and theories indicate that both the quantitative and qualitative characters of the bacterial flora must be ultimately considered in the study of lake types. While a number of observations on the occurrence of bacteria in different types of lakes have been published, these observations have been so fragmentary, and have been made by means of such diverse techniques, that it is impossible to summarize them and draw conclusions concerning the

studies, and to indicate something regarding the adequacy of the techniques used. Brazelle Lake is peculiar, and cannot be readily fitted to the usual classification of lakes. It is small, really a pond rather than a lake. It occurs in the course of a brook which brings in dark brown bog water. The lake is only 2 meters deep, surrounded by marshy ground. The bottom is a mass of decomposing coarse plant remains, with considerable fine material resembling "dy." The water is quite turbid. This lake was selected for observation because of the large

numbers of bacteria found in it by Miss Bere, the only observation approaching those of the Russian workers at Lake Glubokoj. Perhaps "saprobic" would describe the lake better than any other term.

Boulder Lake is also a special case. The lake is broader, but rather shallow (5 meters). It occurs in the course of the Manitowish River, and receives dark brown bog water from the upper reaches of that stream. The organic matter in this water is deposited in the lake; the bottom deposit is "dy"-like. The effluent stream is clear. Apparently the lake is taking care of the organic matter brought to it. It is a good fishing lake, and probably should be considered as eutrophic, although it has some dystrophic characters. The remaining eutrophic lakes named in Table XI are typical enough, and have been described elsewhere.

Of the oligotrophic lakes, Crystal and Weber deserve special mention. They are very similar in size, though Crystal Lake is somewhat deeper. They are seepage lakes occurring close together, with unusually clear water. But Weber Lake had been subjected to fertilization experiments for several years before the observations here recorded were made. This perhaps accounts for the higher numbers of bacteria.

The two dystrophic lakes are typical sphagnum bog pools occurring in a spruce forest, the water still and cold. Mary Lake is much deeper than Helmet Lake.

The data presented in Table XI concern only observations from stations in the open lake, since there are no data available for littoral stations save in Lake Mendota and Lake Alexander. Only summer data are included. The data from the various lakes are therefore comparable from the standpoint of seasonal and horizontal distribution. The counts of periphytic bacteria, and the water plate counts, represent averages of samples from all depths (1, 2, or 3 meter intervals) from top to bottom. Where the bacteria on slides were too few to count, they have been considered as zero. The counts therefore represent averages of a considerable, but varying, number of individual counts. The microscopic counts of

bacteria in evaporated samples of water, taken from Miss Bere's paper, are in some cases based upon a single sample; where samples were taken at different depths or on different occasions, I have averaged the results. But the number of counts averaged is considerably less than in the other three columns. Partly for this reason, and partly because of the nature of the technique, I consider them less accurate than the other data.

One of the most striking features of the data in Table XI is the close correspondence of the plate counts of lake water and the counts from submerged slides. The number of bacteria per square centimeter per day deposited upon the slides is almost directly convertible to bacteria per cubic centimeter which can be cultivated on agar plates. Such is the magic of averages! The numbers of bacteria in the bottom deposit, and those computed from evaporated samples do not correlate so closely.

It will be seen that the eutrophic lakes contain much larger numbers of bacteria than the oligotrophic ones, no matter which of the four methods is used, when averages are considered, but that the figures derived from the submerged slides and from the plate counts of water are more uniformly consistent in classifying the lakes than are the other two sets of figures; *i.e.*, the lowest counts for the eutrophic lakes are higher than the highest counts for the oligotrophic lakes in the first two columns, but this is not true of the third and fourth. The inconsistencies in the microscopic counts from evaporated samples are perhaps to be explained by inaccuracy of the data.

The two dystrophic lakes are widely different. The vertical distribution of bacteria on submerged slides indicates that in these lakes bacterial activity is largely confined to the very surface of the water. It follows that, the deeper the lake, the smaller will be the counts when observations from all levels are averaged. It is perhaps on this basis that we may explain the higher counts from Helmet Lake (of the magnitude of the eutrophic lakes) and the lower counts from Mary Lake (of the magnitude

of the oligotrophic lakes). But both on submerged slides and agar plates, the *kinds* of bacteria found in the dystrophic lakes are obviously quite different from those found in the eutrophic-oligotrophic series. On slides, filamentous iron depositing bacteria such as *Leptothrix crassa* and *Actinomyces ferrugineus* are abundant, though they are entirely absent from the eutrophic and oligotrophic lakes. On agar plates, there are very few chromogenic bacteria, while spore-forming species are dominant, in cultures from the dystrophic lakes. It will probably be discovered that the differences between dystrophic lakes and the others, so far as bacteria are concerned, are qualitative rather than quantitative.

The numbers of bacteria in the bottom muds serve to classify the lakes roughly, *i.e.*, they are high (on the average) in the eutrophic lakes, low in the oligotrophic ones, and intermediate in the dystrophic ones. The counts of bottom bacteria were made contemporaneously with those of the water, identical plate counting methods were used, and they represent about an equal number of samples. The two sets of data are therefore equally accurate. There is not a very good correlation between the counts for water and for bottom deposits. It follows that the numbers of bacteria in the bottom are influenced by factors other than the growth of bacteria in the overlying water.

Henrici and McCoy (1938) made an interesting computation of the relative numbers of bottom and water bacteria of these lakes. By multiplying the average number of bacteria per cubic centimeter in the mud by the length of the column of the sample, and similarly multiplying the average number of bacteria per cubic centimeter in the water by the depth of the lake in centimeters, there were obtained figures which roughly expressed the total numbers of bacteria in the lakes, rather than the concentration only. From these figures, the ratios of total bottom bacteria to total water bacteria were computed. The results for the eutrophic lakes were as follows: Alexander, 5.0; Little John, 1.9; Muskellunge, 0.7; mean, 2.5. For the oligotrophic lakes the

following figures were obtained: Trout, 1.8; Weber, 0.3; Crystal, 0.2; mean, 0.7. The ratios for the two dystrophic lakes were very high: Helmet, 17.1; Mary, 6.1; mean, 11.6. These figures, from relatively crude data, suggest that possibly the ratios of bottom bacteria to those in the total volume of water may eventually prove to be one of the characteristics of the different lake types. This is suggestive of Rawson's (1930) findings regarding the relations between total benthic fauna and the volume of lakes.

Summary of distribution in different types of lakes. Data are as yet too incomplete to warrant any general conclusions regarding the distribution of bacteria in different types of lakes. It seems safe to state that bacteria are more abundant in eutrophic lakes than in oligotrophic ones. From the available data, it seems that eutrophic and oligotrophic lakes form a graded series as regards the numbers of bacteria; and that dystrophic lakes are a special case, probably differing more in kinds of bacteria than in numbers. Numbers of bacteria in the bottom deposits do not correlate well with numbers in the water; it is suggested that the ratio of bottom bacteria to water bacteria may eventually prove significant in classifying lakes.

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SOME RELATIONSHIPS OF PHYTOPLANKTON TO LIMNOLOGY AND AQUATIC BIOLOGY

By G. W. PRESCOTT

ALBION COLLEGE, ALBION, MICH.

THE history of limnology and the growth of the science of lake biology have been, from the very start, so completely interwoven that the two cannot even be thought of separately. There is no intention in this paper to deal with the history of our knowledge of lake phytoplankton, but to do so would be very interesting and illuminating. Such an examination would, for example, serve to establish an understanding of the present complete dependence of phytoplankton ecology on limnology, and at the same time would point out the many ways in which limnology has come to take count of phytoplankton and other aquatic plants.

Although biologists in the last part of the nineteenth century appreciated the determining influence of lake chemistry on the composition of aquatic populations, it was not until the early part of the twentieth century that correlations began to be understood and critically discussed. Limnological studies, especially those made during the past two decades by Birge and Juday, G. M. Smith, Pearsall, Thienemann, Naumann, Wesenberg-Lund, Welch, Ström, Hutchinson, Wiebe, Huber-Pestalozzi, and many others, have resulted in the accumulation of an enormous amount of data.

In this paper the term *phytoplankton* will refer only to algal floras, although we are well aware that certain phanerogamic plants may constitute important plankton components. The presence of a plankton flora in a lake suggests biological problems as intriguing as, or even more so than, those of a land flora. These problems, both of purely scientific interest and also of well-recognized practical importance, are many indeed, and only a few can be considered here.

It is obvious that these problems usually resolve about some phase of plant ecology,

although taxonomy must of necessity serve as a systematizing basis for our knowledge.

When a plant known only from lakes of the Alps, or from Brazil, is next found in western North America or New England, or, when an association of phytoplankton species is found to have a world-wide latitudinal distribution, certain questions naturally come to mind. One of these is, of course: What do the lakes in Brazil have in common with those of New England which permit a certain species to thrive in them and not in others? Or, what are the factors which provide for a geographical distribution of a phytoplankton association?

Certainly the cosmopolitan distribution of many phytoplankters and the wide distribution of little-known or apparently rare species is good evidence that there has been ample time and opportunity for a much more equal distribution of algal species than we now find. In other words, if time and means of translocation were the only factors involved, we might well expect to find nearly the same species of plants in all lakes throughout the world. We do not, of course; and the reasons why we do not are to be found in the combinations of limnological factors which determine aquatic flora and fauna. In fact, we learn from limnology that lakes are even more exacting of their biota components than terrestrial habitats.

While we can follow Thienemann in his classification of lakes, we realize that each lake is an individual entity, a point which cannot be overemphasized. The many interacting factors of an aquatic environment, many of which are based upon or are related to the underlying or surrounding physiographic features as well, provide for innumerable types of habitats. Each lake represents a special and particular combination

FIG. 1. A COMPARISON OF LAKE TYPES IN RESPECT TO A NUMBER OF PHYSICO-CHEMICAL AND BIOLOGICAL FEATURES.*

Type of Lake	Fish	Geological formation	Shape of lake shore	Depth	Sediment	pH	Temperature	Fixed CO ₂	Calcium**	Conductance	Algal flora	Macro-flora
Oligo-trophic.	Low productivity.	Ancient rock.	Few or no shoals.	Very deep, e.g., 30 m. or more.	Little sediment.	Acid. pH 4.5	Temp. average low.	CO ₂ content and reserve low, 2.0 mg per l.	Usually poor; 0.6-12.0 mg per l.	Low, e.g., 5-11 reciprocal megohms. Few electrolytes.	Low quantity; may be nearly absent. Many species; few individuals.	Low quantity. Few species. Little shore vegetation.
	Trout characteristic of primitive lake.	Hard and igneous. Low mineral residue.	Narrow beaches. Sides steep; bottom V-shaped. Low % of water in contact with bottom.		Low mineral deposit.	pH 6.8	Hypolimnion deep.					
Eutrophic.	High productivity. Few or no trout. Perch. Pike. Bass.	Calcareous soft rock. Silica-rich water. High mineral residue.	Beaches. Shallows. Reefs. Gradual slopes. Lake bottom U-shaped. Larger % of water in contact with bottom.	Shallow, e.g., 10 m. or less.	Sediment increasing with age. Gyttja. Silted.	Basic. pH 6.8 pH 9.8	Temp. average high. Epilimnion deep.	CO ₂ content and reserve high, 20-25 mg per l. or more.	High, 40 mg per l.; much higher in European lakes.	High, 100-124. Abundance of electrolytes. Lessens with seasonal increase of phytoplankton as electrolytes are consumed. pH rises.	High quantity. Quality variable. Myxophyceae and Diatoms predominate. Aplanizomon. Microcystis. Anabaena. Gloeotrichia. Lyngbya. Medosira. Stephanodiscus. Peridinium. Ceratium. Oil formers.	High quantity, e.g., 882 kg per sq.m. on bottom. Many species.
Dys-trophic.	High productivity. Smaller size. Perch. Ciscos. No trout.	Recent formations. Old lake beds. Heavily silted bottoms.	Many flats and gradually sloping shore lines. Bottom saucer-shaped.	Shallow.	Heavy sediment. Gyttja. Silted.	Basic.	Temp. average high. No stratification.	CO ₂ high. Variable.			Heterogeneous. Myxophyceae. Diatoms. Filamentous Chlorophyceae.	Scant to heavy growth if dystrophy has proceeded far.
	Low productivity. Yellow Perch. Blue Gill. Bullhead.	Glacial drift. Kettle holes.	With marginal flats, narrow lakes, increasing in width with age.	Shallow to deep. Varies greatly with age.	False bottom frequent. Increased sediment with age.	Basic or acid. pH 5.4 pH 7.8	Wide range in temp. Greatly fluctuates.	Variable, 0.0 to 4.0 ppm.		Variable, 175-190 reciprocal megohms in alkaline bog lakes.	Variable; may have high quantity of Myxophyceae. High in Chlorophyceae species.	Low quantity. Few species in some. Some with dense encrustment from shore line.

* This represents a composite summary from various sources, including the author's observations on North American lakes.
** Nitrates : Oligotrophic lakes, low (0.0-0.001 ppm) ; eutrophic lakes, rich (0.1-0.4 ppm) ; dystrophic lakes, poor ; bog lakes, variable as much as 0.7-1.5 ppm. Phosphates : Oligotrophic lakes, absent or trace ; eutrophic lakes, 0.005-0.1 ppm ; dystrophic lakes, poor (?) ; bog lakes, none. (Na-K)/(Ca-Mg) ratio : Oligotrophic lakes, high (3.2) ; eutrophic lakes, low (1.1).

of factors which, taken together, are able to determine the type of flora and fauna. At the same time we realize that the many dynamic factors in operation result in an ever changing set of limiting factors which thus make possible variations in the fauna and flora from year to year. Nevertheless, a lake may have a combination of characteristics in common with other bodies of water and when such is the case we might well expect to find somewhat, if not quite, similar floras. Thus, when enough lakes have been studied we should expect to find associations of organisms representative of those lakes which have similar environmental factors. This we find in the classifications of Thienemann, and of Naumann; classifications which have proved helpful, particularly for an understanding of European lakes.

In North America we find representatives of the oligotrophic, eutrophic, and dystrophic types. The deep oligotrophic lakes are characterized by a Chlorophycean flora, low in quantity, but often high in number of species, and with a conspicuous Desmid element (Fig. 1).

The shallower, eutrophic lakes are dominated by Myxophycean and diatom floras and, in certain regions of North America,

they are often blanketed with "water-bloom" during the warm season.

The very shallow dystrophic type, of uncertain definitions, supports dense beds of vegetation. The phytoplankton is heterogeneous, although poor in quantity, and mats of filamentous Chlorophyceae are usually present (Fig. 1).

While these types of floras generally are to be associated with the recognized limnological types, we find, as is well known, that very many lakes do not conform, or do so in part only, and invite, therefore, analytical studies. A review of published analyses of lakes in this country and my own observations, lead me to submit, reservedly, the prediction that the time must soon come, if indeed it has not already arrived, when we can and should examine data at hand with the view of drawing up a limnological and phytoplankton classification of North American lakes which will help us to discuss them with more standardized and accurate distinctions. I make this prediction in spite of the fact that some students are pessimistic over the possibility of ever being able to classify lakes according to their phytoplankton types.

We have, for example, certain critically studied bog lakes, the phytoplankton and



FIG. 2. A bog lake, surrounded by a mat of *Sphagnum* and beds of *Chara*.

limnology of which preclude them from the European system of classification (Fig. 1). Oligotrophic lakes, or those with predominating oligotrophic features, are known which show eutrophic plankton; for example, Mountain Lake in Virginia, Lake Nipigon in Canada, Lake West Okoboji in Iowa, and certain lakes in northern Wisconsin and Michigan.

At the same time we find dystrophic plankton in eutrophic lakes and eutrophic lakes with practically no plankton at all. These statements, insofar as my own obser-

used to classify phytoplankton types and to relate them to lake types. Why, for example, does a certain eutrophic lake persistently have an algal population dominated by *Lyngbya Birgei*, while a stone's throw away is one overwhelmingly populated by *Aphanizomenon flos-aquae*? Or, why does one lake have a predominating diatom flora, and one just across the way have no diatoms, but mostly members of the Conjugatae?

These and other similar questions are often answered through the discovery that



FIG. 3. An old lake, passing from eutrophy to heterotrophy.

vations are concerned, are based upon phytoplankton collections made during the summer months only and should be qualified accordingly.

When, and if, a classification of North American lakes should be formulated it should be based upon correlation coefficients of phytoplankton species and limnological features, and should rest as far as possible on a mathematical background. I believe this is possible and infinitely desirable, although patience and painstaking work would be required.

The planktonologist turns to limnology for an explanation of geographical and local distribution. Limnological data have been

there are certain limnological correlations. It is my thesis that these correlations are not, in many cases, the answers we are looking for, but are the clues to the solution of ecological problems. The real questions are only apparently or partly answered by these correlations, and many of our published studies are forced to use the phrases "it seems," or "it is possible."

Notwithstanding the enormous amount of accumulated information, I believe that many more culture studies must be made and the problems carried into the laboratory where the experimental method of research may be added to the extensive field work now being carried on.

CARBON DIOXIDE AND ELECTROLYTES

We can, however, see causal relationships between some limnological features and the nature of the micro-flora. For instance, it is well known and an unfailing correlation that great productivity of phytoplankton is provided by a high carbonate content and a carbon dioxide reserve, such as is found in the eutrophic type of lake (Table 1). This is easily understood, for we know the direct dependence that chlorophyll-bearing organisms have on carbon dioxide. Just what the connection is, we do not know, but it is of some significance that bodies of water in which there is an abundance of carbon dioxide, particularly in tropic waters where there is low oxygen content, have an algal flora made up predominantly of filamentous and branched plants, while unicellular and simple colony formers are typical of well-aerated waters with a low carbon dioxide content.

A rich algal flora, particularly if it is the Myxophyceean type, is a visible index of an abundance of electrolytes. In Wisconsin, and elsewhere in the middle west, *Gloetrichia echinulata* does not occur in every hard water lake in quantities easily visible to the unaided eye. Yet, when it does occur, the relative abundance is evidence that the lake is correspondingly rich in carbonates, and that the conductivity is high.

Also, it is known that there is a definite relationship between calcium and magnesium content of lakes and conductance. Seasonal variation in conductivity accompanies fluctuations in pH and increases in phytoplankton quantity. When the pH is low, conductivity is found to be high, and phytoplankton low (Fig. 1). When phytoplankton increases during the seasonal growth, the conductivity becomes less because of a consumption of electrolytic salts, and the pH rises with the precipitation of carbonates. In certain Iowa lakes the pH may rise from 7.4 to 9.8 during the summer season.

The ratio of sodium and potassium to calcium and magnesium has an important bearing on plankton composition, perhaps more important than is now realized. At

least we find that lakes with a low ratio of alkali to calcium have a diatom and Myxophyceean flora, while a high ratio supports a desmid and a more nearly Chlorophyceean population. For example, the silted lakes of England were found to have a ratio of 1.1. Rocky lakes with a higher Na-K/Ca-Mg ratio (3.2) have a Chlorophyceean flora, particularly rich in desmids as is characteristic of the oligotrophic type of lake.

As Pearsall (1922) and others have remarked, the plankton mass is not so much proportional to the *total quantity* of dissolved substances as it is to the *smallest quantity* of limiting ion present in relation to the *minimum amount required*. This calls to mind the fact that certain elements do not need to be present in large quantities in order to provide for the growth of phytoplankton species, but that if they are not present in required minimum amounts they may be important determiners in the phytoplankton flora. Herein lies a great opportunity for laboratory research.

PHOSPHORUS

In respect to the importance of phosphorus as a determining factor in phytoplankton composition there are some conflicting opinions and evidences. Some limnologists contend that phosphorus has no important part to play in determining phytoplankton productivity and quality. On the other hand, analyses of phosphorus in both marine and fresh water (particularly those made by British limnologists) offer convincing evidence that phosphorus is absolutely essential and is, therefore, a determining element.

Brandt, Fisher, and Harvey have shown phosphorus to be a limiting factor. Harvey (1926) found that phosphorus and nitrogen were completely exhausted in the English Channel with the increase of plankton during the summer season. Wiebe (1930), reporting on the results of the addition of fertilizers to certain bodies of water, states that there is some evidence that phosphorus is a limiting factor in plankton production. Here, although the amount of plankton increased after the addition of fertilizer, no complete differentiation was made between

nitrogen and phosphorus in respect to the effects of the substances on plankton production.

At the same time, it appears from these and other studies that the maximum requirements of phytoplankton for phosphorus are very minute.

Culture studies also, as well as correlations resulting from field work, support the belief that phosphorus is of critical importance. Its abundance in water containing rich plankton growths, particularly in the Arctic, and its seasonal depletion with the increase in both marine and fresh-water plankton, have been established many times. Atkins (1923) found that tropical waters in which phytoplankton was poorly represented, were low in phosphorus, even in the winter. Arctic waters, however, with a high phosphorus content, sustain a phytoplankton flora even greater in amount than is found in the temperate zone in summer.

I have found positive correlations between phosphorus content and productivity of plankton in Iowa lakes (Prescott 1931) and there is some evidence that the difference between one eutrophic lake and another in respect to its flora might be due to the difference in phosphate content. For example, East Okoboji Lake, a shallow eutrophic type, was found to have an average dissolved phosphorus content of 0.031 ppm, even when the Myxophyceae population was enormous. At the same time Spirit Lake, another eutrophic body of water, had an average phosphorus content of 0.0055 ppm. Phytoplankton quantity was much less by hundreds of thousands of individuals per liter in the latter lake. Lake West Okoboji, with some oligotrophic characteristics, had an average phosphorus-content of 0.008 ppm. Here the phytoplankton production was comparatively low and it was predominantly Chlorophycean at most seasons.

NITRATES

The well-known demand for nitrates by phytoplankton, particularly by many of the Myxophyceae species, helps to explain the successful support of these plants by eutrophic lakes. Bodies of water, well sup-

plied with nitrates, or sources of nitrates, have enormous phytoplankton productivity. In fact, the connection is so strong that excessive growths of certain *Myxophyceae* species such as *Aphanizomenon flos-aquae* or *Anabaena circinalis*, may be used as indicators of the presence of organic wastes and high nitrogen content. The turning of a clear, virgin lake into a cesspool of decaying vegetation is repeated over and over where bodies of water come under the influence of human habitation and the cultivation of land.

I have found direct correlation between nitrogen and plankton quantity; and my own culture studies and those of many others all establish nitrogen as an important determiner in phytoplankton distribution and production. As previously mentioned, oligotrophic lakes are low or are lacking in nitrogen and it is of some significance that desmids dominate the phytoplankton in such nitrogen-poor lakes. The lake of this type with a desmid flora is frequently found to lie over ancient geological formations of hard rock and to possess a bottom sediment low in organic content; hence it is one which is poor in nitrogen (Fig. 1).

LIGHT AND TEMPERATURE

Light is obviously a very critical factor in phytoplankton production and one which is modified crucially by suspended matter, color, depth, and latitude. Algal periodicity is of course greatly effected by latitude because of the attending lengths of daylight periods. Productivity is, however, not diminished in northern latitudes for there is an abundance of phytoplankton in certain arctic and subarctic lakes.

To what extent temperature and other factors attending latitude effect quality of phytoplankton we are perhaps unable to state at present. Many species are, however, known only from arctic regions. While temperature is a well-known factor in determining not only distribution but periodicity, we discover that increases or decreases in plankton sometimes attributed to temperature changes are actually due to light fluctuations or variations, which

usually accompany temperature changes, but not always.

For instance, some studies show that phytoplankton may increase in amount during the periods of longer daylight, although, for a time at least, the temperature may be falling off rather than rising (Atkins 1924). However, rises in temperature accompany excessive growths of many species of Myxophyceae and certain Heterokontae, such as *Botryococcus Braunii*, and temperature seems to be the important factor in the development of "waterblooms."

We have the instance of a lake which has a phytoplankton in the winter only, while zooplankton is dominant during the warm, summer period (Griffiths 1936).

An interesting correlation exists between phytoplankton pulses and lunar cycles. From various observations we may cite those of Allen (1920) who found a rise of chlorophyll-bearing organisms at the first quarter, with a climax at the time of full moon, seven days later, after which there was a rapid decline in numbers. The decline in this case was explained by the unusual abundance of Entomostraca, presumably feeding on the phytoplankton.

It is not out of order here to remind that the influence of temperature on plankton distribution, as well as that of other factors, is manifested in the response of species. That is, the results take specific expression. This cannot be overemphasized, and to discuss the effects of environmental factors in this or that group of organisms, or this or that genus, leads only to meaningless generalities. It is necessary to recognize that ecological and limnological studies of phytoplankton should be based upon species adaptations only. Much of our literature is not as helpful as it might be on account of the failure to reduce phytoplankton ecology to a study of species.

CURRENTS

There is space only for the most general remarks concerning the effects of currents on phytoplankton. When lake plankters are carried away by streams there are marked quantitative and qualitative changes. These

changes, involving a decrease in total amount and numbers of plankton species, are in keeping with changes in chemistry and gas content of the water.

The increased amount of sediment, the screening-out action of larger vegetation, and dilution of vital salts by tributaries, all function physically and chemically in reducing the plankton or modifying its composition. Periodicity, seasonal pulses or maxima, and dominant species present entirely different pictures than they do in lakes.

Furthermore, the degree to which phytoplankton is altered in streams depends largely upon the basic chemical nature of the stream and the place in the stream (Chandler 1937). It has been shown that the quantity of phytoplankton is inversely proportional to the slope of the river (Eddy 1934). Phytoplankton changes near the headwater of a stream seem to be due entirely to sedimentation and the screening-out action of larger vegetation. Further down stream even more marked changes are caused by variations in the relative amounts of dissolved nutrients. At the same time, water which was originally low in nutrients at or near the source, might come to support a greater phytoplankton population as it "ages" down stream, with the building up of necessary concentrations of nutrients, particularly nitrogen compounds.

Regarding currents in another sense, *i.e.*, currents set up within a lake, we find many interesting relationships. The availability of the nutrients on the bottom to the bulk of water in the lake is determined by two factors: depth, that is, the bulk of water above the bottom and not in contact with it, and vertical currents. To these might be added a third factor, *i.e.*, that which has to do with the possible distribution of bottom nutrients by rooted vegetation, to be mentioned below.

Where depth is such as to provide for a seasonal overturn of water, the plankton in the upper levels will obviously profit by the distribution of dissolved materials that have been formed by the decay of organic matter on the bottom.

MACRO-FLORA

Notwithstanding some conclusions to the contrary, there is overwhelming evidence that open water lakes which support a rich macro-flora also maintain high phytoplankton productivity (Fig. 1). We have excellent examples of this in lakes of Midwest North America and New England. The work of Rickett (1922) and Wilson (1935, 1937) have given us a mathematical picture of macro-flora production. In the lakes studied, Sweeney Lake for example, I have found a very direct correlation between the large amount of vegetation per square meter, as recorded by Wilson, and the amount of phytoplankton together with the number of component species. This lake showed a greater variety of phytoplankton than any other lake I have ever surveyed, and many of the species were represented by enormous numbers per liter. That there should be such a correlation is only to be expected since the nutrients needed for growth of large aquatics are practically the same as those required by the micro-flora.

Disregarding wave action and other disturbing influences, the nature and chemistry of the bottom sediment determine the type of vegetation. Also, the type of bottom and the surrounding geological features determine the chemistry of the water, and we think we can see many ways in which the chemistry of the water, in turn, determines the nature of the phytoplankton. It follows that a lake with an abundance of organic material on the bottom ("Gyttja" of Naumann, 1917), that is the eutrophic lake with shallows, has a rich macro-flora and, as has been pointed out, the eutrophic lake is the type which usually possesses a correspondingly rich phytoplankton. Aside from the fact that the eutrophic lake with its beds of vegetations and high percentage of shallow water is physically suitable for a large population of fish, it is also the type of lake which has the greatest quality and quantity of food. It has been suggested that large aquatics, rather than phytoplankton, be used as indices as to the adequacy of a lake in fish-stocking programs.

I do not know how much actual evidence

there is, but the statement has been made, and it seems possible, that an abundance of rooted vegetation has, in itself, a very direct determining relationship to phytoplankton production. This relationship, supposedly, is brought about through the nutrients of the bottom being carried into lake circulation by the absorbing action of roots. When plant parts are thrown off, or when the plant as a whole dies and decays in the upper levels, nutrients are released for the use of plankters.

FISH FOOD

In their relation to the food chain of aquatic animals, phytoplankters have important roles in the biology of a lake. First, they are used directly by bottom fauna and by some fish, especially in the fingerling stages. It is known that the gizzard shad, the blunt-nosed minnow, and some other species feed on phytoplankton almost to the exclusion of other forms of food. Kraatz (1928) reports that young suckers, shiners, yellow perch, and wall-eyed pike feed on algae and other plankton. In my own experimental observations to determine the character of food of lake fish, I have found the gizzard shad gorged with *Aphanizomenon flos-aquae* and other Myxophyceae, golden shiner less so, while black bass fingerlings and sun fish showed a mixture of blue-green algae and micro-fauna in the intestinal tract.

Great importance is usually attributed to phytoplankton as the basic food supply of micro-fauna and other fish food organisms. The convincing studies of Bond (1933) on the feeding of the zooplankter, *Artemia* sp. and other similar studies, support the long held and rather general belief that phytoplankton, as such, constitutes the so-called "pasturage" for aquatic animals, both marine and fresh water. In this connection we should cite the work of Martin (1922, 1923, and 1928) on the food of the oyster. One of Bond's summarizing remarks is: "It is perfectly obvious that zooplankts generally do ingest a considerable quantity of particulate matter, and that a large proportion of the ingested material is

actually digested. This is certainly the case with *Artemia*—it seems reasonable to conclude that the same holds true for copepods, Cladocera, mosquito larvae—and the rest.”

On the other hand, some students, both in Europe and this country, especially since the published work of Pütter (1909), contend that fish food organisms do not feed directly on phytoplankton, but use, rather, dissolved organic and colloidal substances. Hence, large aquatics as well as land flora surrounding a lake, contribute to the food of water animals as much as or more than the phytoplankton. From the many studies made in this connection we may cite the work of Clarke and Gillis (1935) for evidence. These workers found that the copepod *Calanus* survived and molted in large numbers when cultured in water containing bacteria and nanoplankton. Whereas, cultures in membrane-filtered water died rapidly. Also it was shown that sterile filtered water would not support *Calanus*. Furthermore, it was found that the dissolved products of decay of organic matter are not easily assimilated by animals nor even by the bacteria.

Convincing evidence is presented by various workers and data obtained by their laboratory experiments challenge the conventional concept of the place of phytoplankton in the food chain. However, the interesting work of Krogh (1931) points out that some fauna require more food than is possible to be obtained from dissolved organic substances. One study for instance, showed that only 10 mg per liter of organic substances to be present in the water with an energy quotient of 40 Cal. It is contended that this is far below the amount required to support the micro-fauna concerned. Also it has been shown in some other studies that algae do not liberate any carbohydrate material and hence cannot contribute substances to the dissolved food supply (Krogh *l.c.*). Where synthesized matter has been found in algae cultures there is no proof that it was not derived from dead and decayed plants.

The experimental work of Krizenecky

shows that mussels and tadpoles are able to survive on dissolved organic matter, but only when it is present in concentrations greater than the occurrence in nature. However, it is worthy of note that, in the case of mussels and some other organisms, absorption of dissolved organic matter occurs through the intestines and not the gills.

Using indirect evidence to support the importance of dissolved organic matter as food, we may turn to the studies of Huff (1923) on Vadnais Lake in Minnesota. Here it was shown that increases in zooplankters and phytoplankters occurred quite independently, and that a decrease in the phytoplankton had no effect whatever on the animal population, as would be expected if the fauna were dependent on phytoplankton for food. Huff concludes that while phytoplankton may be important in oxygenating the water or in furnishing food for *some* zooplankters and bottom animals, the micro-flora, as such, cannot be regarded as ultimately basic in the food chain.

Conflicting lines of reasoning may develop from those studies which indicate that the fauna of a body of water require more food than can be shown to be available from quantitative studies of the plankton. However, in depths of the ocean where dissolved substances are most abundant there is a zoological desert. (Krogh *et al.* 1931). This of course suggests the dependency of micro-fauna on phytoplankton.

We remember that usually deductive arguments are used to support the notion that phytoplankton is of basic importance. Its value is judged frequently by quantitative studies of zooplankters *before* and *after* the peak of phytoplankton pulses. Those not in agreement with the importance of phytoplankton would claim, I suppose, that the increases that do occur in the micro-fauna after a phytoplankton pulse are due to the increase in the food in the form of substances created by the decay of phytoplankton and also by the accumulation of organic matter from shore vegetation and surface drainage.

In connection with the food relationships

of aquatic animals, mention should be made of the work of Welch (1916, 1924) and Frohne (1938) in Michigan who have shown the dependence of many fish-food organisms on higher aquatic plants.

When analyzed, the problem seems to me to be one for which insufficient data are collected to establish a correct idea as to the dependence of animals on phytoplankton. Weighing the various lines of evidence, it would seem desirable to answer the question of whether micro-fauna use phytoplankton and particulate matter for food, or dissolved organic substances, by reducing the problem to one of determining which species of animals tend to feed on particulate matter (perhaps nannoplankton alone), which use dissolved matter, and which use both particulate and dissolved matter. In other words, generalizations as to the use or disuse of phytoplankton in the food chain cannot be drawn from present data, and those which we now hold should be set aside, at least temporarily.

UNBALANCED BIOLOGICAL CONDITIONS

Phytoplankton species which enter into "waterbloom" associations thrive very successfully in warm water (25° to 30° C), particularly if there is an abundance of carbon dioxide in reserve and an adequate supply of nitrogen compounds. Under these optimum conditions their excessive growth may come to interfere in the biology of a lake to a serious degree and oftentimes they are, either directly or indirectly, the cause of a great deal of economic loss and many objectionable conditions.

The greatest pests are Myxophycean species, especially those species which multiply rapidly, float high in the water (possibly because of the pseudo-vacuoles which these plants contain), and which possess sticky mucilaginous sheaths or colonial envelopes. *Aphanizomenon flos-aquae* and *Microcystis aeruginosa* are two such species which very frequently enter into destructive waterbloom associations in this country. In Lake East Okoboji, in Iowa, these plants periodically form dense, "soupy" masses of vegetation and thick, floating scums which decay rapidly in the intense light and heat of mid-

day. Spirit Lake, nearby, also has dense growths of blue-green algae during the summer period, but here the flora is made up of species which do not float high in the water but remain suspended throughout and which do not possess sticky sheaths, such as *Lyngbya Birgei*, for example. Consequently this lake is spared the climax conditions which are very disturbing in Lake East Okoboji.

One of the results of these overwhelming growths of phytoplankton is the death of fish, produced either directly or indirectly. Occurring, as they do, in the warm seasons when the oxygen content is low in any case, the enormous numbers of plants withdraw more oxygen from the water than they return through photosynthesis. Myxophyceae as a class are poor oxygenators. During warm, still nights (with oxygen release by photosynthesis interrupted) they may entirely deplete the oxygen supply or reduce it to an amount which will not support fish life. In these lakes the oxygen may be decreased from 4.5 to 5.5 ppm to 1.5 or 2.0 ppm within a day or a few hours. The exhaustion of the oxygen brings about the death of both micro-fauna and phytoplankton and the decay by bacteria of this mass of organic matter quickly reduces further the oxygen content and then fish and other aquatic animals are suffocated. It is not uncommon in the Middle West of North America to find small lakes or bays of larger lakes with scarcely a living creature after an excessive growth of algae has broken up and decayed. The writer has seen the shore line whitened with windrows of tens of thousands of fish destroyed in this manner. All fish organisms are found to be dead, even the bottom-living *Chironomous* larvae, and the lake becomes a veritable graveyard and "desert." Hence economic loss of game fish is considerable and there are drastic effects on the general biology of the lake.

Fish and game agencies undertake to increase, by various means, the oxygen content of such infested lakes, often at great expense, in order to prevent the wholesale death of fish.

It is apparently possible for algae to

bring about the death of fish through the liberation of substances toxic to them during the decay process. I have some experimental data at hand (Prescott 1932) to support this and we have numerous references in the literature. When highly proteinaceous blue-green algae undergo decay, sufficient quantities of hydroxylamine and other derivatives are produced to poison any fish caught in the shallow water of a bay by masses of decaying algae. In my

boating are all made unpleasant or impossible because of nauseating odors and the disagreeable condition of heavily infested water.

Infrequently our attention is called to the death of cattle, claimed to be due to drinking from bodies of water containing dense growths of blue-green species. Until recently these cases have not been subjected to much scientific analyses, but the work done in Minnesota by Fitch *et al.* (1934)



FIG. 4. Fish dead on the shore of a lake after the break up of winter ice. Suffocation, the cause of this wholesale death, was due in part to the growth of blue-green algae which, under the circumstances of winter conditions, was excessive. This scene is duplicated in late summer when large masses of algae decay and bring about the destruction of fish.

controlled experiments, tanks of water were used. One tank was kept as a control. Varying amounts of decayed blue-green algae were placed in the other tanks. A number of different species of fish in these tanks died at intervals (except in the control tank), although necessary oxygen content was maintained.

The ability of phytoplankton to destroy recreational sites is well known. In this respect they are often not only a nuisance but an economic menace. Bathing, fishing,

establishes that a causal relationship actually exists. Laboratory experiments have shown that while alive certain Myxophyceae species liberate toxic substances (or substance) and that these are capable of killing laboratory animals when the water in which these plants have been growing is injected. Whether or not these substances are also lethal for aquatic animals is a question upon which no research has been done, apparently.

Besides the objectionable effects of phyto-

plankton just mentioned, these plants are capable of ruining water supplies for domestic and commercial use. When alive, and more especially after they have decayed, a number of species of algae impart obnoxious tastes and disagreeable odors to impounded waters which these plants find very suitable for luxuriant growth. Also, they seriously interfere with filtering systems and in these several respects bring about economic loss.

PROBLEMS

In conclusion the writer wishes to outline what seem to be some important problems open for much desired research.

1. We need to know more about the life history of phytoplankton species; the factors which underly their unexplainable pulses; the causes for their periods of abundance and decline. For many we do not know in what form they pass their dormant condition, if indeed they have one. We do not know where they pass their dormant condition: in shallow waters, on the bottom in deep water, or suspended as plankters? Information on some of these points will throw light on the local source of phytoplankton. Also, a study of these problems may help us to answer the question as to the phylogenetic history of plankters. Did they migrate from, or are they hold-overs from, ancient seas with salinity much less than now? Or, did they develop first in shallow fresh water, warm and rich in nutrients, and then migrate into open water as plankters? On these points we can only offer conjectures at present.

2. Although we now possess much information on both lake chemistry and phytoplankton composition, we need to seek out the actual determining factors responsible for phytoplankton distribution. We know only a few of these factors. I am not entirely in agreement with some students who state that it is impossible to find phytoplankton associations in definite correlation with lake types. To be sure each lake has its own combination of determining factors. Yet we find certain species or groups of species occurring in similar or nearly similar

lakes. Where species seem to fail to serve as indices of lake types or qualities of lakes it may well be that the failure is entirely due to our inability to recognize those characteristic lake qualities of which these species are representative. I believe we can establish some species or groups of species as indicators which will be as reliable (within limits) as are terrestrial plants when used as indicators of edaphic factors or other environmental conditions.

3. Another intriguing problem and one which has far-reaching practical importance has to do with the place of phytoplankton in the food chain of aquatic animals. If it can be established that micro-fauna feed primarily on dissolved organic matter or colloidal substances, then our notions and our textbooks will need revision. Furthermore, if this should be true, the quantity and quality of phytoplankton cannot be used as fairly direct indices and guides for the stocking of lakes with fish. Programs involving the addition of fertilizers for nurse lakes will find no significance in the increase of phytoplankton as a result of the added nutrients insofar as food for fish is concerned. In order to complete a useful picture of the value of phytoplankton in the food chain, a series of coordinated experimental studies should be made to involve the following:

a. A determination of the amount and quality of plankton food required to produce a measured amount of micro-fauna.

b. A determination of the quantitative and qualitative values of these same species of micro-fauna in the food chain of fingerlings of various important species of fish, expressed in weights and numbers of individuals of fish produced.

c. A determination of the quantity of food needed to bring these same fish to maturity so that it will be known how much of what kinds of food are necessary to produce a given number of fish pounds.

With such data we would be able to evaluate a lake in terms of its fish productivity and fish-stocking programs could be carried out all the more efficiently.

4. The taxonomy of phytoplankton must

go forward. Great sections of our country are relatively unexplored in this respect. We need to know what is there, and furthermore we need to know what plants are present in our lakes at all times of the year. It is unfortunate that so many ecological and taxonomic studies are based on summer collections only. If we are to re-classify our lakes in respect to their limnological characteristics, and attempt a classification in respect to their phytoplankton types, then our familiarity with species must be maintained and we must have expert advice on the definition and the listing of species. Before sound ecological generalizations can be made we must have more data on the occurrence of algal species.

In this connection the writer wishes to suggest that when phytoplankton species are reported from various parts of our country, that herbarium records be kept. This is becoming increasingly more important. If possible, herbarium material should be placed in a number of central museums where they may be more available for the students of algal taxonomy and ecology. Taxonomy is of basic importance and should be maintained on the same scientific level as are the other sciences. Therefore, the work of the taxonomist should be conducted in such a way that it may be repeated and confirmed.

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THE ZOOPLANKTON IN RELATION TO THE METABOLISM OF LAKES

By WILLIS L. TRESSLER

UNIVERSITY OF BUFFALO, BUFFALO, N. Y.

INTRODUCTION

THE important part played by the animal members of the plankton is difficult to overestimate. It is they which form an intermediate link between the producing green plants of the water, or perhaps between the available organic matter, and the larger aquatic animals. The organisms comprising the zooplankton include the Copepoda, Cladocera, Rotifera, and Protozoa, together with other groups of somewhat lesser importance such as the Ostracoda and Phyllopoda. The problem with which limnologists are concerned is the attainment of a complete knowledge of the structure, behavior and interrelationships of these animals. This knowledge is of interest for its own sake and it is also important in a practical way as a tool in the increased production of fish life. Our information regarding the zooplankton was until recently of little practical importance, since nothing could be done about a lake or pond poor in plankton. Within the past few years experimentation with fertilizers has shown great increases in plankton production, and as a direct result in added rate of growth of fish, so that now we may say that not only are we familiar with the disease but in many cases we are able to effect a cure.

Before going into the well-known facts concerning the life and habits of the zooplankton, let us concern ourselves briefly with the ancient origin of fresh-water plankton in general. According to Welch (1935), there are two possibilities: plankton originated in ancient geologic ages in the ocean, or, as some believe, it may have had a fresh-water origin in shallow pools. We know little about the composition of the ancient seas and it is possible, according to one theory, that these waters were quite fresh and have gradually become saline in

the course of time. If this were true, plankton could have migrated from the relatively fresh-water seas into the inland waters without the barrier imposed by a difference in salinity. Since then the two realms have developed along diverging lines, each with its own plankton. As to the age of fresh-water plankton, there is a great difference of opinion; some authorities contend that all fresh-water plankton in temperate regions goes back only to the ice age, when it migrated from the Arctic regions. Others hold that fresh-water plankton is of much greater antiquity than the ice age and that while it may have been forced to leave certain areas, it reentered the old regions after the end of the ice age. In any event, fresh-water plankton must have come into fresh water before the arrival of the higher aquatic animals, since these forms are dependent upon the plankton for food. The question of the routes taken by plankton in entering fresh water has caused considerable speculation. Three theories in general have been advanced to explain the path of the migrants. The tropical origin theory has few adherents. The other two possibilities are that of a polar origin under conditions of greatly varying salinity and temperature, where the organisms became accustomed to a varying environment, and the theory put forth by Wesenberg-Lund (1926) that modern pelagic forms have been developed and are still being developed from bottom dwelling and littoral organisms.

DISTRIBUTION OF ZOOPLANKTON

While plankton is found in almost all natural waters, its distribution is subject to wide variation. Geographical differences, differences due to the depth of the water, variations at different locations on the lake, and seasonal changes are all very marked.

The distribution of zooplankton forms depends upon the type of environment to which the particular organism is suited, the species in question, and to many other factors. The same species may also show considerable variation in distribution in one lake from its distribution in other lakes. There are, however, certain general statements which may be made for the distribution of zooplankton and it is these that we shall now consider, together with some more recent observations.

Most of the limnological investigations have been carried on in temperate lakes, while very little work has been attempted on tropical waters and practically none on the lakes of the far north, particularly in North America. In Europe, most of the lakes of Norway, Finland, and the Baltic countries yield a good plankton crop, and if it is assumed that conditions in fresh-water lakes are similar to those of polar seas, then it may be said that the polar waters contain a more abundant plankton than those in the tropics and more than most temperate waters. Johansen (1931) and others have made collections in the region of Hudson Bay and in the Northwest Territories (Marsh 1920) and reported several kinds of plankton crustaceans, some of which were distinctly northern forms, while others are found all over the continent. No quantitative work was done, and, as far as the writer has been able to determine, none has been attempted on the lakes of extremely northern regions. Here is certainly an unpioneered field for future limnological research.

In tropical lakes there are somewhat more data to work with. The recent publications of Ruttner (1931) on the lakes of Java and Sumatra, of Worthington and Ricardo (1936) on the East African Lakes, and of others, have shown that many tropical lakes support a fairly generous plankton population. In Lake Edward, in East Africa, for example, eutrophic conditions were found, although most of the life was concentrated above the thermocline, and in Lake Bunyoni there was an abundant macro-plankton fauna although little micro-plankton. Dr.

Woltereck has been kind enough to supply me with a summary of conditions in the lakes of the Philippines, Celebes, Bali, and Java which were obtained during his Wallacea Expedition in 1932 and which have not as yet been published. He states that in the warm waters of tropical lakes, in general, one finds no greater abundance of individuals or of species than in temperate lakes. This is in great contrast to the conditions in the tropical rain forests in Celebes, for example, where over 1,000 different species of trees are to be found. For most of the groups of animal and plant plankton there is often a considerably smaller number of species in tropical lakes than in temperate waters. Diatoms, *Cyano-phyceae*, and Desmids are just as differentiated as they are in the temperate regions, although cosmopolitan species are fewer in number than the tropical forms. This is also true of the Rotifera and to a certain extent of the Ostracoda. The copepods play a dominant part in tropical lake plankton, much more than do the Cladocera, which when compared with temperate lakes are much reduced in numbers. In the tropical lakes one finds many endemic forms of Diaptomidae while the Cyclopidae are much less differentiated (Brehm 1937). The Cladocera are found in tropical waters in limited numbers. There are a number of species of *Diaphanosoma*, few *Bosmina* and almost no Daphnids. (Daphnids were found only on the Island of Flores in the tropics and subtropically in Hawaii.) It will be seen that Asia shows no parallel in the tropics to the very great variety of *Daphnia pulex*, *D. longispina* and *D. longiremis* in North America and of *Daphnia cucullata* or of *Bosmina coregoni* in Europe. The picture, strange to say, completely changes if we consider the larger plankton, especially the Decapoda, which are partially littoral and partially pelagic in the tropics and enormously differentiated. In Towoeti Lake alone were found seven endemic decapods (Woltereck 1937). The same is true of the pelagic fresh-water fish of tropical lakes and for the non-pelagic Mollusca. In Lanao Lake, in the southern Philippines,

more than a dozen endemic Cypridians were found; in Africa in Lake Victoria there are over 50 endemic Cichlidae. There is thus a genetical relation to be noticed in the marked difference between the larger and the more or less microscopic inhabitants of tropical fresh water. The earlier accepted idea that the small plankters of tropical fresh water were mainly cosmopolitan has, however, been proved to be false. There must be some other reason for this remarkable difference.

The geographical distribution of zooplankton in temperate regions is by no means completely known. There are certain crustaceans whose range has been known to be restricted to the northern or to the southern half of the temperate region or to deep cold-water lakes when found in more southerly regions. Others are cosmopolitan and are found all over the world. The rotifers in general are of this type. The *Diaptomus* group, on the other hand, is very restricted in the distribution of its species, most species being endemic to the region in which they are found. In White Lake, North Carolina, a peculiar distribution of crustaceans has very recently been reported by Coker (1938). In this shallow, clear-water lake, only two calanoid copepods (no Cladocera or rotifers) live limnetically. *Cyclops nanus* and other species were found living near the bottom. These forms have not previously been found south of New York. Of the calanoid copepods, *Diaptomus minutus* was known mainly from deep lakes. Similarly the ostracod, *Candona croghaniana*, was originally found in temporary shallow pools in Georgia, but since then it has been found on the bottom of the deepest parts of Lake Mendota, in the St. Lawrence River, and in other places. So that, as Coker points out (1938b), the appearance of anomaly in many of the distribution records comes from an inadequacy of knowledge of the fresh-water fauna of this country. There is great need for more study of the fresh-water crustaceans.

In another type of environment, the shallow lakes of the arid regions, Hutchinson (1937) has found a peculiar association of

a Daphnid with a large and a small Diaptomid. This situation has been found to be characteristic of extreme cases of aridity in various parts of the world. It is believed that these three forms feed on the bacterial and organic matter found in the suspended mud.

The vertical distribution of zooplankton, except in shallow lakes and at the time of the spring and fall overturns, is very complicated and varies so much in different lakes, with different organisms (and even with the same species in different lakes) and at different times of the year, that only general statements can be made. Almost all of these statements are subject to exceptions. Welch (1935) gives a summary of certain tendencies in the vertical distribution of zooplankton as follows: "(1) a greater occurrence of the Sarcodina in the lower waters; (2) preference of the Dinoflagellata for upper waters; (3) general scattering of the Ciliata; (4) selection of different levels by the young and adult stages of certain crustacea." Cold-water forms tend to keep to the deeper waters of lakes unless the supply of oxygen becomes depleted, when they are driven into the upper regions. A study of vertical distribution of plankton groups in 60 samples taken in 36 lakes and reservoirs of New York State (Tressler and Bere 1934, 1935, 1936, 1937, 1938) shows no relation between the position of maximum abundance of a group in one lake and that of the same group in another lake. The Protozoa had their average maximum abundance in all the lakes at 5.3 meters, while the range was between 0 and 15 meters. The others ran as follows: Copepoda, average, 7.1 meters, range, 0-30 meters; Nauplii, average, 9.9 meters, range 0-35 meters; Cladocera, average, 6.5 meters, range 0-25 meters, and Rotifera, average 7.5 meters, range, 5-40 meters. The average depth of the lakes was 22.6 meters and the range, 5-50 meters. These variations were caused by differences in the species in the various lakes, differences in time of day and season at which the sample was taken (all were taken between June and September) and to differences in individual lake conditions.

Variations in the vertical distribution of individual species in different lakes has been shown to be the case in several instances. In Lake Nipissing, Langford (1938) found that *Diaptomus oregonensis* migrated from the lower strata of the hypolimnion after midsummer and sought the upper regions. This was correlated with oxygen depletion and increase in carbon dioxide in the bottom layers. These movements led to a series of experiments using a small vertical gradient tank designed by Dr. Fry. It consisted of a small aquarium, 15" high, in which vertical stratification was produced by cooling and heating devices and changes in carbon dioxide and dissolved oxygen were produced at will. Samples of water at various depths could be withdrawn for analysis; thermometers in the walls gave temperatures at various levels and the plankton could be counted at any level by means of a magnifying glass. The results showed that *Daphnia magna* and *Cyclops bicuspidatus* moved from a region of high carbon dioxide to a lower one and from a low concentration of oxygen to a higher one. The movements counteracted such factors as higher temperature and a positive geotropism in the case of *C. bicuspidatus*. These movements were comparable to those of immature *Diaptomus oregonensis* in the lower strata of Lake Nipissing. An increase in carbon dioxide of 12–15 ppm and a decrease in oxygen to 4.3 ppm seemed to start these movements. It should be pointed out here that these movements were not complete evacuations of the lower depths, and this was also true in the experiments; some individuals remained under conditions from which others migrated.

In each lake, or perhaps in each type of lake, every organism has its own preferred level. This is true to a certain extent in groups of plankton, is true of species, and Woltereck (1932) has shown that, in the Wisconsin lakes with stratified water, each stratum has its own peculiar race of Daphnids.

The factors influencing the vertical distribution of zooplankton are divided into two groups by Rylov (1935) as follows: (1) mechanical factors, including the spe-

cific gravity of the plankton and the effect of currents, and (2) biological factors, including temperature, light, food relationships, pH, dissolved salts, and dissolved organic matter. Langford (1938) believed that light was the most important factor in Lake Nipissing but that it was qualified by other factors such as food, chemical constituents, temperatures, in some cases the wind, gravity, age and sex of the plankton, specific differences, and finally by actual depletion at a certain level or levels due to consumption by some plankton feeder, such as the Cisco. Not enough is known about the food of zooplankton to state definitely how much this factor influences vertical distribution. Many plankters feed upon phytoplankton which are more or less confined to the upper layers, but if Pütter's (1909) theories are right, and there has been some evidence favoring them lately, the presence or absence of phytoplankton need not determine the presence or absence of food since organic matter may be used. The influence of carbon dioxide and oxygen has already been discussed. Temperature seems to be a controlling factor in some cases; for example, *Diaptomus oregonensis* and *Limnocalanus* seem to prefer cooler waters and *Epischura* warmer. The thermocline is also a barrier to migration in some forms, although if the recent evidence of the periodic dissolution of the thermocline in Lake Windermere given by Ulyott and Holmes (1936) holds for other lakes, the thermocline may not always be the formidable barrier it has been thought to be. Whether higher or lower temperatures decrease or increase the sensitivity to light of an organism is a disputed question. Langford (1938) found that higher temperatures lessened sensitivity in nauplii and *Epischura*, while Welch (1935) states that the opposite is true. In Lake Nipissing on a few occasions the wind acted in making the distribution uniform for most organisms and in depressing the thermocline, thus scattering many of the plankton groups. Gravity affects all organisms heavier than water and most forms have to actively exert themselves to remain in a fixed position.

It was generally believed by the earlier

workers that distribution of plankton was uniform over a body of water. This conception of regularity in the horizontal distribution of plankton has for some time been definitely disproved by many investigators. In some small lakes, it is true, seemingly uniform distribution has been reported, but in the great majority of large lakes the horizontal distribution is very irregular. Recently, linear series of trap samples taken from one end of a lake to another have been carried out in one Ohio lake (Buckeye) (Tressler, unpublished) and in three New York lakes (Canada, Otsego and Chautauqua) (Tressler and Bere 1935, 1936, 1938). These investigations have confirmed the irregular distribution of zooplankton. Within the past year some similar studies on Lake Nipissing have been reported by Langford (1938). Trap samples at a series of depths were taken at 10 stations within a radius of three-fourths of a mile. Ten samples were also obtained from 8 meters at one station. *Diaptomus* and nauplii were more variable horizontally at 8 meters than in one spot. *Cyclops*, *Epischura*, and *Bosmina* were not so much more variable horizontally at 8 meters. No trend was found when 10 stations were taken in a linear series. Ricker (1937a) in Cultus Lake, British Columbia, however, has obtained different results. He found the horizontal distribution to be approximately the same in the immediate vicinity of the sampling station as over the entire lake. *Cyclops* alone showed a more variable distribution. These conflicting results are probably due to a difference in the lakes themselves (Cultus is much smaller than Nipissing) and also possibly to different collecting methods employed (Ricker used a closing net).

Horizontal irregularities in plankton distribution may be caused by a number of factors acting either singly or simultaneously. Welch (1935) states that wind action is the most important and lists as contributing causes inflowing streams, irregularity of shore line, depth, general flowage areas, currents, undertow currents, swarms,

predators and, indirectly, diurnal migrations.

Another phase of horizontal distribution has been followed by Chandler (1937) who determined the fate of lake plankton in streams originating from lakes. It has been well known that plankton decreased in amount as it passed downstream, but previous work had been done on streams which had other tributaries or which had pollution areas. Chandler worked on streams in Michigan which were without tributaries or pollution areas. His results showed that the greatest decrease occurred in areas which had a heavy growth of vegetation. One such place showed a 70 per cent decrease in 20 meters! When the vegetation was removed, the decrease in plankton was no longer conspicuous. It was found that the vegetation strained out the plankton or that the plankters actually clung to the material on the stems or debris. Here they apparently settled to the bottom. Temperature, pollution, dilution from tributaries, or change in chemical relations were found not to be factors in this decrease in the streams which were studied.

Seasonal variation in the quality and quantity of zooplankton is a subject regarding which it is impossible to make general statements. The total quantitative seasonal variations are to be discussed later under productivity; variations in the seasonal distribution of the various groups depend to a large extent upon the species comprising the group under consideration, and also vary with the particular lake concerned. Most of the studies of zooplankton throughout the entire year have been made on a few lakes in southern Wisconsin and Michigan. Burkholder (1931) followed the phytoplankton through the year in Cayuga Lake and also followed to a certain extent the chemical relations. Recently a series of samples collected monthly throughout the year has been taken on Chautauqua Lake (Tressler, Wagner, and Bere, unpublished). With these exceptions, however, most of the work has been undertaken in the summer months only, with here and

there a few scattered winter observations, most of which are not quantitative. It seems to me that here is one of the most important problems, the seasonal determination of zooplankton in various parts of the world and the correlation of its distribution with various physical and chemical factors.

In most lakes, there is, for most organisms, a spring and fall maximum, but that these maxima may vary somewhat in the exact time at which they occur in different lakes, and in the same lake for different years, has been observed in a number of instances. We may briefly illustrate this by a comparison of the various groups in Lake Mendota in the year 1916 (Birge and Juday 1922) and Chautauqua Lake in 1936 and 1937. In the copepod group both lakes had *Cyclops* and *Diaptomus* as dominant forms with *Cyclops* more numerous. In Mendota the copepods continued in fair abundance throughout the year with a maximum in the spring (April to June) and again in November. The copepods in Chautauqua were reduced to almost zero during the winter and reappeared in fairly large numbers in May. Another maximum occurred in the fall in November. Nauplii were present throughout the year in both lakes but in Mendota their maximum number appeared in June and July with a very short period of great abundance in November, while in Chautauqua there were two maxima, one in late spring and again in early fall. The Cladocera in Mendota exhibited spring and fall maxima and in Chautauqua their distribution was similar to that of the Copepoda, although their spring maximum did not start until June. Rotifera were abundant the year around in both lakes. In Mendota the maxima appeared in June and January, while in Chautauqua large numbers were found in May and again in September, with only average abundance in between. The Protozoa in Mendota showed spring and fall maxima. In Chautauqua there were very few protozoans and these were found in the very early spring (March and April) and again in September.

The cause of seasonal changes seems to be due to numerous factors, the most important of which are the periods of spring and fall overturn and the consequent mixing of the bottom waters rich in organic matter with the water of the entire lake. Spring and fall rains and the resulting inwash, temperature differences, light, dissolved oxygen, and other environmental factors also undoubtedly play a part. Phosphorus and silica have been thought to be limiting factors, but there is so much conflicting evidence, particularly in the case of phosphorus, that it is doubtful if very much



FIG. 1. Collecting limnological samples on Chautauqua Lake, February, 1937.

significance can be ascribed to these two factors. A coincidence between carbohydrates and crude proteins and the spring and fall maxima of Cladocera has been found in a Danish lake (Krogh and Berg 1931). Very likely seasonal distribution will be found to be caused by different factors in different lakes although the most important causes will probably be similar.

The fluctuation of zooplankton from year to year has been reported by Ricker (1938) who found considerable variation in numbers over a ten year period in Cultus Lake. This is possibly due in this case to varia-

tions in the salmon run resulting in varying amounts of fertilizer added by the dead salmon. In a year of unusually large abundance of salmon the duration of the plankters' period of abundance was found to be correspondingly increased. Young (1935) also found the life of Flathead Lake not constant. In 1893 Forbes reported the zooplankton as consisting mainly of *Daphnia longispina*, while recently it was found that this form was far inferior in numbers to *Cyclops* and usually to *Diaptomus*. Forbes noted *Epischura* as common, while today it is unknown. *Epischura lacustris* was also common in Lake Michigan 40 years ago, but is absent now. The remainder of the life of Lake Michigan was found by Eddy (1927) to be about the same. Other lakes in which changes have been noted are Red Lake near Luzern (Baehman 1931) and Devils Lake, North Dakota. The last two variations were undoubtedly caused by chemical changes in the lake, but in many other cases no such explanation is available.

An interesting accompaniment of seasonal changes is the change in body form which many cladocerans and some rotifers exhibit. In most cases this cyclomorphosis takes the form of added spines or an increase in length of spines, or helmets, as the summer approaches, but in some rotifers there is a reduction in the length of the projections at this time. The change is comparatively rapid, usually occurring in two or three weeks and takes place as a cumulative addition in length in each succeeding generation and not as a process of growth in one individual. Various factors have been assigned as the cause of this unique phenomenon, the most probable explanation being that it is caused by the combination of change in viscosity of the water and a change in the factors in the environment, such as food relations.

The present status of our knowledge of zooplankton distribution is well summed up by Worthington and Ricardo (1936) who state that "Much work on the measurement of controlling factors in the field and experimental work on the behavior of dif-

ferent organisms must be performed and correlated before a complete and general explanation can be given of the distribution and movements of plankton."

PLANKTON PRODUCTIVITY

The limnological measurement of the usefulness of a lake is based upon its production of plankton, and lakes have been classified by Naumann and Thienemann (1929 and 1931) on this basis. Thus we have the highest producers known as eutrophic, the lowest as oligotrophic, and in between mesotrophic. Within the last few years, however, several modifications have been made in this classification and lakes have been found which do not exactly fit into the original scheme. Hutchinson (1938) has suggested that some system of lake typology should be formed which would take into consideration both the trophic conditions in their original sense (Naumann 1929) and factors due to the morphology of the lake basin. These two factors vary independently. Lundbeck (1934) distinguishes between primary, or edaphic, oligotrophy and secondary, or metamorphic. A shallow lake with a poor supply of nutrient materials would be relatively oligotrophic, but the hypolimnion might be so small as to produce an oxygen deficit in the bottom water. Also, in eutrophic regions a deep lake may have such a large hypolimnion that no oxygen deficit may be formed. In secondarily oligotrophic lakes the volume of water is so great that it requires a long time to accumulate enough salts for the lake to become productive. Also, accumulation of sediment may cause high productivity in immature lakes, such as in Green Lake, Wisconsin. In alpine lakes in Europe no amount of reduction of the hypolimnion would cause secondary entrophy due to the extreme lack of nutrient salts, and in extremely productive lakes, such as some lakes in the tropics, an enormous hypolimnion would be necessary to reduce the oxygen deficit appreciably. Thus in the Philippines it was found (Woltereck and Tressler unpublished) that no oxygen existed below 10 meters in most of those lakes which were

visited. The extreme case was found in Ticob Lake, 80 meters deep, with no oxygen below 4 meters. Large accumulations of hydrogen sulphide were present in the hypolimnion of most lakes of the islands. Worthington and Ricardo (1936) also have found that the East African lakes do not fit into the old classification. They are eutrophic with high productivity, but oligotrophic in the sense that oxygen is present in appreciable quantities at all depths. This is contrary to Thienemann's conclusion that true oligotrophy could not exist in the tropics and that all tropical lakes were eutrophic. High alkalinity was found to be a factor in the unusual conditions in the East African lakes. Woltereck found that there are eutrophic, mesotrophic, and oligotrophic lakes in the tropics which may be very near one another. The extremes, however, are much more pronounced than in temperate lakes. Eutrophy, when it is reckoned throughout the year, is greater, and the same is true of extremely oligotrophic lakes such as the great Lake Towoeti in Celebes where the oligotrophy was so great that the Secchi disc was visible at 24 1/3 meters below the surface.

In temperate regions the extreme oligotrophic lakes tend to be in the northern part of the north temperate zone or in high mountains. Flathead Lake in Montana which has been studied by Young and others (Young 1935) shows a typical oligotrophic mountain lake with deep cold water and low plankton productivity which is mainly distributed in the upper third or fourth of the lake. Mountain Lake, Virginia, (Hutchinson and Pickford 1932), is oligotrophic in the chemical composition of the water and mud in the character of its phytoplankton, and also in the poverty of its littoral and bottom fauna. The productivity of the epilimnion, however, is eutrophic due to the shallowness of the lake basin. Hutchinson (1937) in studying the extremely high mountain lakes of Tibet, where the altitude ranged from 4,241 to 5,297 meters (nearly 17,500 feet maximum), found that many showed considerable plankton production and were to be considered as mesotrophic.

The reasons suggested were the greater aridity of Tibet, which caused greater concentration of nutrient materials in the lakes, and great solar radiation, which also probably increased productivity.

Plankton productivity of lakes showing unusual conditions has been studied by several workers in Michigan, particularly. Raymond (1937) found that a marl lake had small plankton production, the plankters being apparently restricted to those which could withstand the conditions present in a marl lake. Large amounts of calcium were believed to be detrimental to plankton productivity due to the formation of bicarbonate which robbed carbon dioxide and influenced the pH as a consequence. The deposition of calcium carbonate also formed a type of bottom unsuited for rooted aquatics which would result in an absence of turnover of nutrient materials. Welch (1936a and 1936b) also found low productivity in both acid and basic bog lakes. In the basic bog lake, while the productivity was low, a much larger number of species of plankters was found than had previously been reported for bog lakes. The productivity decreased as the summer progressed. The same conditions were found in a retrograding bog lake (Welch 1938). Here there were few rooted aquatics, but their number showed some increase with the returning alkaline conditions.

Various indexes of productivity have been suggested. Klugh (1926) proposed that the abundance of rooted aquatics might be an index of productivity, and this contention is supported by the work on marl and bog lakes to a considerable extent. Very recently Hutchinson (1938) has found that in some lakes, at least (Green, Mendota, and Black Oak in Wisconsin and Foresö in Denmark), the rate of development of the absolute oxygen deficit in the hypolimnion, per square centimeter of hypolimnion surface, is proportional to the mean standing crop of plankton per unit area of lake surface. This supports Ström's (1932) earlier method in harmonic temperature lakes. This calculation can thus be used as a measure of productivity where gravimetric de-

terminations of total plankton are not available.

By far the best and most accurate index of plankton productivity of a lake is the gravimetric determination of total plankton as organic matter, and it is astonishing that this important tool has not been more widely used by limnologists; most of our data from this source comes from the work on Wisconsin lakes. Thus Birge and Juday (1934) reported an examination of 529 lakes. They found that the centrifuged or particulate organic matter of the surface waters ranged from 230 to 12,000 mg per cubic meter, with a mean of 1,360. Some lakes showed little or no seasonal variation, others as much as threefold. The annual variation ranged from zero to eight times, but most of the lakes showed annual variations within the seasonal limits. Drainage lakes were 45 per cent more productive than seepage lakes, due to the incoming waters carrying minerals and other constituents. Greater productivity was observed in shallower lakes, the greatest being from lakes 2 to 3 meters deep. Other factors were the size and the shape of the lake basin. The complete circulation of water and repeated use of raw materials seemed to explain the larger yield of shallower lakes. The vertical distribution showed considerable variation; the largest amount occurring at the surface in 10 per cent of the lakes over 18 meters depth, at the bottom in 34 per cent and at intermediate depths in 56 per cent. In 43 lakes the maximum was between 3 and 10 meters; in 20 lakes below 10 meters but not at the bottom. The organic matter was found to consist of 37 per cent crude protein, 4 per cent ether extract, and 59 per cent carbohydrate. Soft-water lakes were found to give smaller amounts of organic matter than hard-water lakes (2-4 $\times$). Trout Lake showed 128 kg per hectare, Nebish 61.3, and Mendota 240. (The summer average for Chautauqua Lake in 1937 was 118 kg per hectare.) The dissolved organic matter, as contrasted with the particulate matter removable by the centrifuge, was found to range between 16,000 and 17,000 mg per cubic meter in the aver-

age lake, of which 8 to 9 per cent was made up by the plankton. The extreme figure obtained was over 50,000 mg per cubic meter. The main source of the organic matter was the plankton plus mud and higher plants. External sources were humus, marsh, and peat extractives. Seepage lakes had much less organic matter and averaged 3,000 to 6,000 mg per cubic meter, of which 15 to 18 per cent was plankton.

The organic matter and its distribution has been studied in a few New York lakes (Tressler and Bere 1936, 1937, 1938). In the 19 lakes in which determinations were made the maximum amount occurred at the surface in 31 per cent, at the bottom in 31 per cent and at intermediate depths in 37 per cent. Twenty-one per cent of the lakes showed a maximum amount at 5 meters. Values ranged between 420 mg per cubic meter and 3,690. Seasonal variations are considerable in most lakes and follow rather closely the periodicity of plankton abundance. Chautauqua Lake, for example, showed three peaks, one in the fall, one in the spring, and a third and by far the largest in late August. The actual values varied from 1,037 to 2,343 mg per cubic meter with 1,728 the average. As a rule there is a distinct correlation of the organic matter with the plankton counts, although in some cases there seems to be no relationship between them. Meehan (1937) in some work on bass ponds found no correlation between the dissolved organic content and the average phyto- and zooplankton counts and suggested that this indicated that a large part of the source of food supply for zooplankton is closely associated with bacteria rather than phytoplankton. Horizontal variation of organic matter in lakes has been rather infrequently reported. In New York State two linear series of 10 samples taken from one end of the lake to the other have shown substantially the same results, viz., a marked increase at the outlet end. This increase is a gradual cumulative one as one proceeds down the lake. In Otsego Lake (Tressler and Bere 1936) organic matter at 3 meters' depth showed a 112 per cent increase, while in Chautauqua

Lake the increase was 285 per cent, or from 1,300 to 5,000 mg per cubic meter. The accumulation of material as the water slowly flows down the lake probably accounts for this concentration at the outlet end. The knowledge concerning the geographical distribution of organic matter is, as far as I am able to determine, completely a blank and here lies, I believe, another most important field for future research—the determination of organic matter in lakes other than those of the temperate zone, together with the vertical distribution in such lakes.

DIURNAL MIGRATIONS OF ZOOPLANKTON

Vertical migrations of zooplankton have been discussed in other papers and it will suffice here to very briefly review some of the recent work and trends in this field, particularly from the standpoint of the zooplankton itself. The early ideas of a simple vertical migration from bottom to the surface during the night have been largely exploded and in their place very complex movements involving both up and down migrations have been found to take place in many instances. Very recently, Langford (1938) has reported the results of studies of the migrations of five groups of plankton in Lake Nipissing. Here *Diaptomus minutus* showed a complex diurnal movement due to differences in the movements of the two sexes. In intense light both sexes were at a maximum at the surface. With decreasing light, the males moved downward; females remained and only gradually left the upper waters to appear in greatest abundance at dawn at the thermocline. With the absence of light the males again returned to the surface and remained until dawn, after which they moved down and were replaced at the surface by the females. Later on the sexes were equalized at the surface. Other workers have also noted different migrations of the sexes. Southern and Gardiner (1932), however, found no difference in the movements of the sexes of *Diaptomus gracilis*. Male *Cyclops* showed greater abundance at the bottom at all time, but especially between sunset and midnight. Here the fe-

males were most active in diurnal migration. Kikuchi (1927) found that the females of *Diaptomus pacificus* were more active in migration and were at a maximum at lower levels than the males. Worthington and Ricardo (1936) found a case of reverse migration in Lake Rudolph in East Africa, where *Diaptomus* was near the surface during the daytime and descended to deeper water at night. Nicholls (1933) reported similar reversals in the normal migration of *Calanus finmarchicus* in the ocean. In each lake each species and the sexes of each species seem to show individual reactions to environmental conditions. In Lake Nipissing *Diaptomus minutus* also showed great variation in the extent and type of its migration during the season (May to September). At times there was no change in its position while at others a definite movement toward the surface was observed. Seasonal changes in the diurnal migrations of plankton have not been followed to any extent and further work might possibly throw added light on the causes of migrations. Langford believed that light was the most important factor in causing migrations, but that it undoubtedly was modified by other environmental factors. This was shown by the variations in migration at different seasons. In 1903 Juday stated that the problem could be solved only by complete observations covering a considerable interval of time, and this opinion has been amply justified in the period since.

The present situation in regard to our knowledge of the migrations of zooplankton is summed up by Worthington and Ricardo (1936) who state in substance that the older and simpler theories to explain diurnal migrations did not completely explain all movements. New work has been concerned mainly with a measurement of physical conditions in the water, such as light and temperatures, and a laboratory study of the behavior of different animals. Instantaneous readings of intensity and composition of light and temperature can be made at any depth and can be correlated with plankton hauls with nets simultaneously. Laboratory experimentation has shown that dif-

ferent organisms behave differently under the same conditions. Also, in many cases animals in the laboratory behave differently from those in their natural habitat. This fact makes it extremely difficult to correlate laboratory and field work. "It seems probable, however, that the ultimate picture of planktonic behavior will come from such a correlation."

COLLECTION METHODS

The accuracy of the results of quantitative estimations of plankton has been questioned by many workers. Plankton catches are subject to certain errors which may be enumerated as follows (Ricker 1938): (1) lack of uniformity of horizontal distribution, (2) ability of plankters to avoid capture, (3) collection errors, (4) errors in enumeration. Ricker (1937) has worked out certain statistical limits, but as Langford (1938) points out these limits apply only when the distribution of plankters is known to be random. Langford believes that the effects of horizontal variation can be overcome by taking a number of duplicating series and that greater accuracy can be obtained by making counts of a smaller number of organisms from each or a fraction of mixed samples from one depth than by counts on single samples. In lakes with even bottom contours, a single central station will give a fairly good representation of the whole lake, but in lakes with rough and uneven bottom contours a considerable difference in the quantity of the pelagic plankton has been shown to exist (Southern and Gardiner 1926 and others). Southern and Gardiner (1926) and others observed that the net plankton was less in daytime than at night, and they believed that this was due to the ability of the plankters to see and avoid the net. This difference occurred most markedly in the upper lighted areas. They found an extreme ratio of 2.4 between night and day catches in Lough Derg in the case of *Daphnia longispina*. Ricker, however, found no difference in the day and night abundance of *Epischura*, which lives in the upper waters. The ability of plankters to see and avoid the net

was further studied by Ulfyott (1936) who used black nets. He found that black nets reduced the difference in some cases but had no effect for most species. It is believed that individual species exhibit differences in ability to see and swim away from the net or trap, and that these individual differences in behavior must be known before a general explanation of the differences in day and night catches can be given. Worthington and Ricardo (1936) found this to be true in Lake Rudolph where *Diaptomus* crowded near the surface showed no difference in day and night catches, while the Cladocera in deep portions of the lake showed marked differences in quantity.

Collection errors are largely due to the type of collecting apparatus used even when such apparatus is handled in the most careful manner. The old vertical haul closing net had the advantage of covering all the water from the bottom to the surface, it was easy to handle and transport but had the very serious drawback of being very unreliable and variable in the amount of water strained. Ricker (1938) found that even when handled with the utmost care a new No. 20 net after five hauls had its efficiency decreased as much as one-third or even one-half. A No. 10 net gave good and fairly consistent results for the larger forms, but failed to capture most of the smaller zooplankton (one-half of the *Synchaeta* and one-fourth of the nauplii). It has also been shown that there is a great difference between vertical hauls and stage hauls, vertical hauls giving more plankton. Langford in comparing the closing net with the plankton trap found wide ranges in efficiency at different depths and for different distances of vertical haul. In a haul from 2.5 meters to the surface the efficiency for various organisms varied between 55-84 per cent with a mean of 65 per cent, while in the least efficient haul from 10 to 5 meters the net caught only 10 per cent of the plankters captured by the trap. It has been suggested that some of the material may be spilled when the net closes, and that such losses account for the greater efficiency when the net is hauled from shallow depths to

the surface. The most accurate and efficient collecting apparatus for zooplankton is the plankton trap of Birge and Juday (Juday 1916) which strains a definite quantity of water and has such a large opening that probably few plankters escape it. Its one disadvantage is its bulkiness. This is inconvenient but is soon forgotten by the manipulator after a few lakes have been in-

also to reduce the sampling error. Plankton pumps are ideal especially where large quantities of water must be strained, but they are by far the bulkiest and most unwieldy of collecting devices requiring a good-sized boat and preferably a power drive. For Protozoa, the regular water sampler and centrifuging through the Foerst centrifuge seems the best method. Very re-



FIG. 2. Raft used to obtain limnological samples in the tropics. Sanpaloe Lake, Philippine Islands, April, 1932

vestigated. This trap in the 10 liter size has been used since 1931 by the New York State Biological Survey with very good results. In the Philippines the trap was used on many lakes, even on those which had to be reached by a 10 or 20 kilometer hike into the mountains. Last summer (1938) it was tried in salt water in the bays of Long Island. Here, two 10 liter samples were taken at each depth due to the comparative scarcity of zooplankton forms and

cently Clarke and Bean have devised a collecting device consisting of a small cylinder with net attached which may be towed at any depth and the actual amount of water strained measured by a propeller and counter. In tests, this device has shown results which compare very well with collections made with the plankton trap, and it has the added advantage that it may be towed in multiple with other units all on the same line. It seems a little complicated,

but has demonstrated its ability to catch most of the larger forms in spite of the comparatively small opening.

The remaining source of error, due to sampling, fractioning and counting, is probably not great and, with ordinary care and an occasional recheck, can be reduced to a minimum. Rather elaborate statistical studies of errors in plankton collection and enumeration have been undertaken by Ricker (1937a) and other Canadian limnologists. These studies, while they are of great interest, seem to be of less practical value to the limnologist. Sampling of a body of water is not assumed to be an exact science, and this has well been illustrated in some remarks by Allen (1938) in commenting on the accuracy of certain plankton catches in the Gulf of California. He states, "Under such considerations it should be apparent that the rigid accuracy more or less erroneously attributed to all scientific activity is actually unattainable and that the investigator must be content with something less than the popular ideal. As a matter of fact, this condition is not as bad as it seems or as it may be made to appear to be. The life of the investigator himself is not a result of rigid accuracy. It is a series of compromises, readjustments, and approximations. In fact, all life is like that to a greater or lesser degree and even inanimate Nature is not free from appearances of uncertainty or confusion. And, if a determination of the characteristics of a population in the ocean could be made with rigid accuracy for a given instant, the terms expressing this accuracy might be widely misleading if applied to the population present an hour or a day later. . . . To really know Nature one must sacrifice something of mathematical accuracy at times and depend upon a series of approximations (which, paradoxically, will lead to a nearer approach to accuracy than would be possible by the use of extreme refinements)."

THE UTILIZATION OF PLANKTON BY FISH

The examination of stomach contents has shown that many fish utilize plankton as an important element in their diet. It has gen-

erally been believed that fish simply strained a great quantity of water and separated out whatever was in it. Some recent work, however, has shown that in some fish, at least, this is not true and that there is an actual selection of food by the fish. Battle *et al.* (1936) found that the herring captures each individual plankter. This can also be noticed in goldfish when *Daphnia* are put in the aquarium. Every plankter is hunted down by individual capture. Ricker (1937) found that the sockeye salmon seemed able to distinguish between individual plankters and even showed individual preferences. He confined 10 fish in the same limited environment and found that seven of them took almost all *Daphnia*, three took *Cyclops* as well, while one of the three took only *Cyclops*! Ricker points out that individual preferences for different organisms may cast some doubt on the reliability of average food consumed in series containing a few stomachs only. The kind of food eaten was also found to vary with the season; in May and June, when the fish were small, *Cyclops* and *Bosmina* were fed upon. Later in the summer the food was mainly *Daphnia*, and in winter *Cyclops* and occasionally considerable numbers of *Bosmina* were taken. The sockeye salmon continued to feed mainly on plankton to the third year.

PROBLEMS FOR FUTURE INVESTIGATION

During the course of this discussion a number of lines of investigation, in which much more work can be done, have been pointed out. In summary these are as follows: further study of zooplankton organisms and their distribution; pioneer quantitative work on the plankton of little known regions, particularly in the tropics and in northern regions, more work on seasonal distribution of plankton and organic matter, especially in unknown regions; further study of seasonal changes in the diurnal migrations of zooplankton and the development of a "perfect" collecting device for macro-plankton.

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THE MICROSCOPIC FAUNA OF THE SANDY BEACHES

By ROBERT W. PENNAK

BIOLOGY DEPARTMENT, UNIVERSITY OF COLORADO, BOULDER, COLORADO

INTRODUCTION

ONE of the most recent lines of investigation in limnology is that of the ecology of the microscopic organisms inhabiting the capillary waters of sandy beaches. During 1936 and 1937 studies in this field were carried out at a number of Wisconsin lakes and the majority of our remarks, which are by no means conclusive, are based on the results of this work. These researches have settled few questions, but have demonstrated the existence of many biological complexities in this interesting environment.

In the mind of the biologist the word "sand" is almost invariably associated with "desert." If, however, we examine the uppermost few centimeters of the exposed sand adjacent to the water's edge, a rich and varied microscopic flora and fauna will be discovered. Figs. 1 and 2 show two such typical Wisconsin lake beaches.

The organisms in the sand, or psammolittoral, as it has been called, are primarily the genera and species encountered in true aquatic environments. Numerically, the rotifers, copepods, and Tardigrada, or "water bears," constitute the majority of the Metazoa. Fig. 3 is an optical section of a small portion of a beach showing the size relationships of the sand grains and these organisms.

PHYSICAL FACTORS

In contrast to the chemical and physical conditions prevalent in lake waters, conditions in beaches are subject to rapid and drastic fluctuations. Let us consider first some of the physical factors at work in beaches.

The organisms within a beach are subject to two opposing currents of water: a slow upward current caused by the rise of capillary water in the sand and its evaporation

at the surface, and an intermittent, comparatively vigorous downward current resulting from waves and rain beating upon the sand. Nevertheless, in many beaches rich populations of organisms are found in situations over which waves wash only rarely, if ever.

The amount of water in the sand, particularly in the surface layers, varies over a wide range. However, mean values for 30 series of determinations of the water content of the top centimeter of sand show approximately 80 per cent saturation at 100 cm from the edge of the water, 40 per cent saturation at 200 cm, and 20 per cent at 300 cm.

As would be expected, the slope of a beach governs the width of the inhabitable zone of the sand. A beach having a slope of 8° from the horizontal may have a populated zone 150 cm in width, while a beach having a slope of 3° may have an abundance of organisms as far back as 300 cm from the edge of the water.

The size of the sand grains constituting a beach determines the size of the spaces in which the organisms live, but no significant differences, qualitative or quantitative, have been found in the psammolittoral populations which can be attributed definitely to differences in sand-grain size. The proportion of pore space is practically uniform (about 40 per cent of the total volume), whether or not the sand in a beach be fine or coarse, heterogeneous or homogeneous in composition.

Temperatures of the sand are governed by a number of factors. The most important of these are lake-water temperature, air temperature, amount of capillary water and its evaporation, wind, and sunshine. What little we know of beach temperatures support the following conclusions:

1. During the course of an average summer day the temperature of the surface of the damp sand may vary as much as 10°C ; frequently the range is probably greater, especially during other seasons of the year.

2. The surface layers, where most of the organisms are found, heat up and cool off more rapidly than the deeper layers.

3. Near the edge of the water the sand

the particulate organic matter deposited on shore by waves, wind, and rain. Determinations of total organic matter in 18 different beaches gave means for the individual locations which ranged from 0.4 to 6.5 mg per 10 cc of sand. Single samples sometimes contained as much as 80 mg. The particulate organic material is of two types: a finely divided organic debris present in



FIG. 1. Beach on the north shore of Trout Lake, Vilas County, Wisconsin.

temperature is governed largely by the lake water temperature.

4. Even under a hot sun a small amount of water in the sand, 25 per cent saturation for example, is sufficient to keep the temperature low enough to be tolerated by the organisms. Sand containing this amount of moisture was never found to rise above 32°C . Of the rate of evaporation from the surface of the sand very little is known.

In addition to bacteria and algae, an important food source for the organisms is

all beaches and a coarser material, less generally distributed, composed of bits of leaves, aquatic vegetation, and insect remains. In the majority of cases the sand within 100 cm of the lake averaged less than 3 mg of particulate organic matter per sample. This low organic content is due to wave action which serves to keep the inner beach washed comparatively clean. Of course, the amount of particulate material in any one beach may vary over a wide range, but the data thus far gathered show



FIG. 2. Beach on the north shore of Day Lake, Vilas County, Wisconsin.

no constant correlation between the amount of organic material in the sand and the populations of organisms. However, a beach having less than 0.5 mg per 10 cc of sand will support only a small population. On the other hand, in outer regions of some beaches where quantities of humus become mixed with the sand, few organisms are found, even though plenty of interstitial water might be present.

CHEMICAL FACTORS

A small amount of work has been done on the chemistry of the capillary water contained in the uppermost 8 cm of the sand. For these studies sufficient quantities of water were sucked out of the sand with a 25 cc volumetric pipette having a small piece of silk bolting cloth over the lower end to prevent the entrance of sand particles. Because the interstitial air introduced bubbles into the samples, determina-

tions of dissolved gases could seldom be made on water samples taken beyond 100 cm from the edge of the lake. It would be valuable to devise methods of sampling the small amounts of water present between 100 and 300 cm where a large portion of the organisms are found.

From the point of view of life in the sand dissolved oxygen is an important factor. Studies have shown that the greater the distance from the lake the lower the oxygen content. In several instances no oxygen could be demonstrated in the capillary water at the 100 cm stations. Also, in a number of beaches the sand at distances of 200 and 250 cm, at depths of 4 cm and lower, contained ferrous compounds, indicating anaerobic conditions. Such situations are well known in sea beaches.

The free carbon dioxide in the capillary water had considerable variation, depending upon prevailing chemical, physical, and

biological conditions. In all cases, however, there was significantly more free carbon dioxide in the capillary water than in the adjacent lake water. In determinations made at 13 beaches the free carbon dioxide in the sand at the edge of the water ranged from 2.0 to 9.5 ppm, while at the 100 cm stations the amount varied from 4.5 to 38.0 ppm. It is likely that the more frequent wave action near the edge of the water discourages bacterial action and the consequent production of carbon dioxide. There were greater quantities of free carbon dioxide in beaches protected from wave action than in exposed beaches.

Varying amounts of bound carbon dioxide were also found, even at different stations in the same beach. In general, how-

ever, the capillary water contained more than the lake water, sometimes as much as 50 per cent more.

In nearly all cases the capillary water was more acid than the adjacent lake water, from .1 to 1.3 pH units. Undoubtedly the hydrogen ion concentration is subject to variations even during the course of a single day, in spite of buffer mechanisms presumably present in the sand. These variations are yet to be determined.

As for dissolved organic and inorganic materials, it was found that the majority of beaches are environments appreciably richer in these substances than the waters of the lake. This is particularly true on the shores of soft-water lakes. Much fundamental work can be done on the absorp-

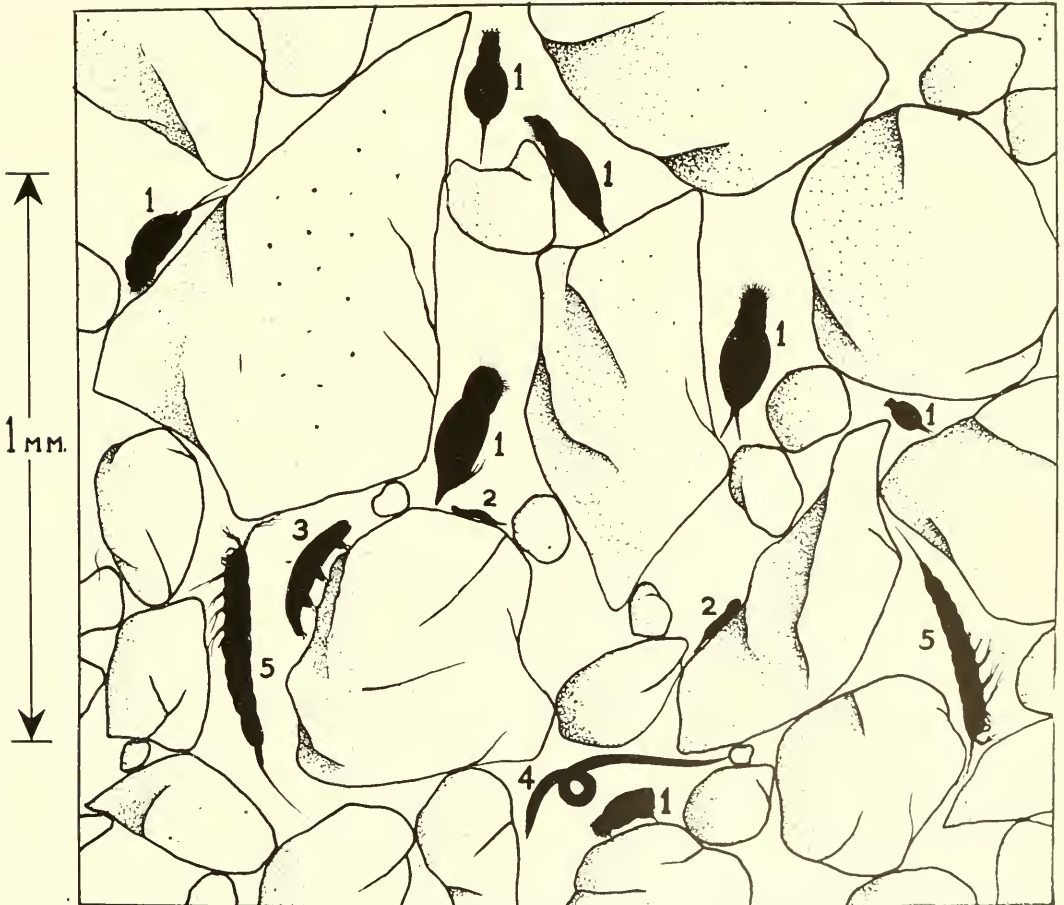


FIG. 3. Optical section of a small portion of a sandy beach showing relative sizes of sand grains and some of the common species of microscopic Metazoa. 1 = rotifers, 2 = gastrotrichs, 3 = tardigrade, 4 = nematode, 5 = harpacticoid copepods.

tion and interchange of ions between beach sands and lake.

Fig. 4 shows some typical chemical conditions in the capillary waters of a beach in relation to the adjacent lake water.

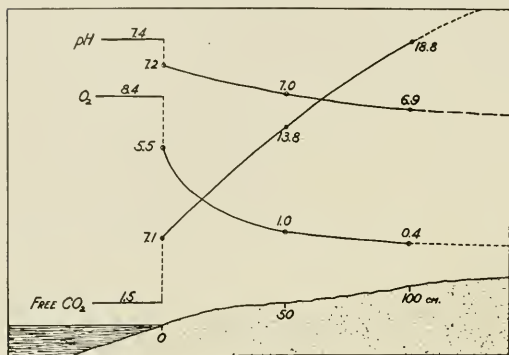


FIG. 4. Typical chemical conditions in capillary water. Values to the left of 0 cm are for the lake-water within 50 cm of the water's edge. Curves beyond the 100 cm station are theoretical.

THE ORGANISMS

The psammolittoral Metazoa were collected by means of brass tubes 14 cm in length, and having cross-sectional areas of 10 sq cm. At various distances from the edge of the water the tubes were thrust vertically into the sand. Then, with the contained cores of sand, they were removed and corked at both ends. In the laboratory the corks were removed and each core of sand was pushed out of the top of its tube by means of a plunger inserted at the lower end. In this way successive one-centimeter slices of the damp sand could be removed at the upper end. By a series of washing and concentration processes, the organisms were removed from these 10 cc sand samples and preserved for later examination.

BACTERIA

During the past summer investigations at the Trout Lake Limnological Laboratory in northeastern Wisconsin have shown that beaches contain unusually large numbers of bacteria. These studies justify the following generalizations:

1. 80 to 90 per cent of the bacteria were found in the top 3 cm of sand.

2. Horizontally, they were most numerous between 75 and 150 cm from the edge of the water, being 10 to 20 times as abundant there as in the rest of the beach.

3. The numbers varied between 33,000 and 8,000,000 per cc of sand.

4. In contrast to the situation in lake waters, the sand was found to contain large numbers of anaerobes, sometimes as many as 19,000 per cc of sand. A common maximum was 5,000.

PROTOZOA

Like the bacteria, the Protozoa were most abundant in the top 3 cm of sand between 75 and 150 cm from the edge of the water. The numbers found there ranged from 300 to 50,000 per cc of sand. Frequently there were found between 7,000 and 12,000 per cc. Among the 30 genera found, some were Sarcodina and Ciliata, but the small flagellates, both green and colorless, were by far the dominant group. Often great crops of euglenoids, in sufficient numbers to give the sand a distinct greenish color, were encountered in the beaches of soft-water lakes. We believe that the Protozoa of beaches present a wide opportunity for the protozoologist from the points of view of physiology and ecology as well as taxonomy.

Vigorous wave action served to lower bacterial and protozoan populations markedly, but in a few days the numbers returned to normal.

TARDIGRADA

A group which has been almost entirely neglected in this country are the Tardigrada, or "water-bears." These organisms form a large part of the psammolittoral population in the Wisconsin beaches. All of the specimens which were closely examined were found to belong to the genus *Macrobiotus* (Schultze), but only a small percentage were examined. Their food habits in beaches are unknown, but presumably they subsist on desmids and filamentous algae and perhaps occasionally on the body fluids of rotifers and nematodes. From data gathered at 18 beaches it is evident that the tardigrade populations in the sand cannot be ascribed to simple ecological relationships. Table I shows the

Lecane bulla, *Trichocerca multierinis*, *Scaridium longicaudum*, *Cephalodella forficula*, and *Cephalodella cra.*

Thirty-nine species are known to be confined almost exclusively to the sand environment. Some which were abundant in the Wisconsin beaches are: *Dicranophorus hercules*, *Euchlanis arenosa*, *Lecane inquieta*, *Lecane paraelosteroocerca*, *Trichocerca insolens*, and *Wierzejskiella velox*.

Of the psammophile forms the following were abundant: *Cephalodella gibba*, *Lecane*

an average of only about one individual per sample was found. Although the relative distribution of the rotifers in the sand was fairly uniform it was found that the numbers in a single beach may vary as much as fiftyfold over a period of time. There is great need for the causes of these variations to be worked out.

The horizontal distribution was quite characteristic, but there were certain interesting diversities. The mean distribution of rotifers for four series of sand samples col-

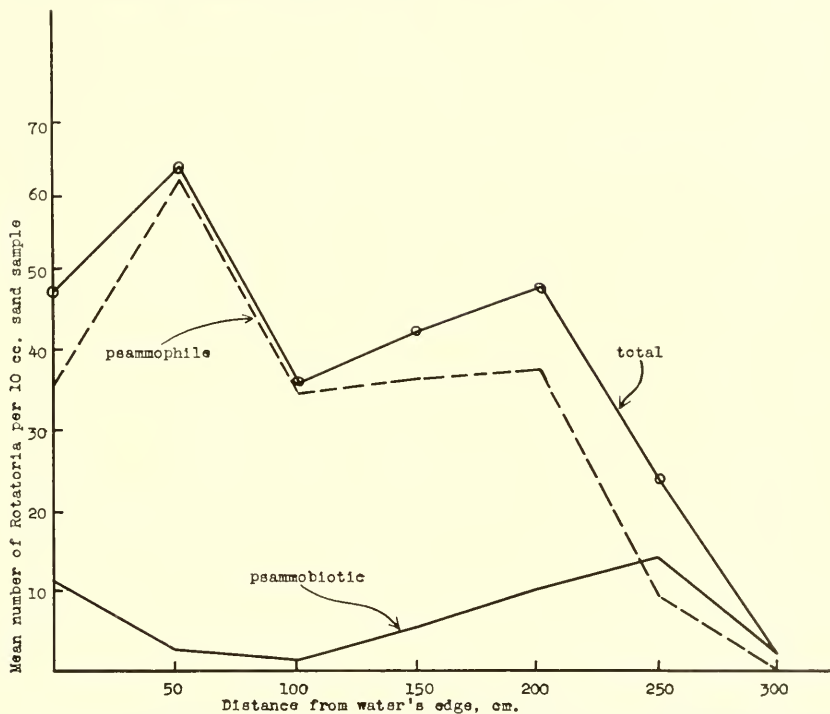


FIG. 5. Mean horizontal distribution of Rotatoria to a depth of 8 cm for four series of 10 cc sand samples collected at a beach on the south shore of Trout Lake, Vilas County, Wisconsin.

closteroocerca, *Lecane hamata*, *Lecane lunaris*, *Lecane scutata*, *Lepadella patella*, *Trichocerca intermedia*, and *Trichocerca tenuior*.

Table III shows the populations of Rotatoria in three typical series of samples. The greatest population encountered during the course of this study was found in the top cm of sand 100 cm from the edge of the water at a beach on Trout Lake on July 19, 1936. This 10 cc sand sample contained more than 11,000 specimens. The smallest population occurred in a beach on Lake Superior where

lected at a beach on the south shore of Trout Lake to a depth of 8 cm is shown in Fig. 5. This beach was characterized by a small proportion of psammobiotic rotifers, with maxima of about 11 and 15 at the 0 and 250 cm stations, respectively, while more than 30 psammophile specimens per sample were found between the edge of the water and the 200 cm station. At the 300 cm station the total number of rotifers was only about two per sample.

In contrast, the mean values for a beach on the northeast shore of Muskellunge Lake



FIG. 6. Mean horizontal distribution of *Rotatoria* to a depth of 8 cm. for four series of 10 cc sand samples collected at a beach on the northeast shore of Muskellunge Lake, Vilas County, Wisconsin.

in 1937 showed comparatively small numbers of psammophile rotifers (Fig. 6), with maxima of 25 and 24 per sample at the 0 and 100 cm stations. Psammobiotics numbered 37 per sample at the edge of the water and 59 at the 100 cm station. At the

150 cm station the total number of rotifers dropped sharply to only 15 per sample and at the more distant stations less than five were present.

Fig. 7 shows the mean horizontal distribution of the rotifers for all samples col-

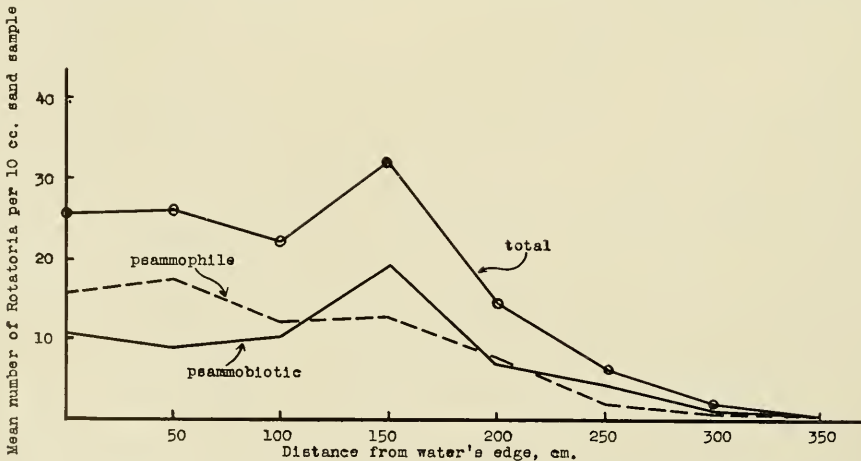


FIG. 7. Mean horizontal distribution of *Rotatoria* to a depth of 8 cm for 49 series of 10 cc sand samples collected at 18 different beaches in Wisconsin.

lected during this study. Within 100 cm of the edge of the water the psammophile species were more numerous, but beyond that distance the psammobiotic forms were dominant. The total numbers ranged from 26 per sample at the edge of the water to 22 at the 100 cm station, 33 at the 150 cm station, and then decreasing to about 15, 6, and 2 at the subsequent stations, with less than one per sample at the 350 cm station.

Numerous sand samples were taken from the submerged sand near the edge of the water but only 31 per cent as many rotifers were found there as were found directly at the edge of the water.

Table IV shows the mean vertical distribution at six beaches. The beach studied

only recently pointed out by Wilson that the sandy beaches of lakes and oceans, and brackish areas, support a great number of copepods, particularly harpacticoids. These sand-loving copepods are very small and worm-like; they swim feebly and depend chiefly on continual wriggling movements to get about in the interstitial water. In contrast to the situation in marine beaches where many species are found, only three species are known from lake beaches; two of these, *Virgircella paludosus* Mrázek and *Parastencaris starretti* Pennak were found on the shores of a single lake, Starrett Lake. *Parastencaris brevipes* Kessler occurred in all beaches except the one at Lake Michigan.

Table V shows the distribution of the

TABLE IV

MEAN VERTICAL DISTRIBUTION OF ROTATORIA IN SIX DIFFERENT BEACHES TO A DEPTH OF 8 CM.
RESULTS ARE EXPRESSED AS MEAN NUMBERS OF SPECIMENS PER 10 CC SAND SAMPLE.

Depth, cm	Beach					
	Michigan	Mendota	N. Trout	Muskellunge	Starrett	Day
1	17	24	65	316	303	159
2	23	10	16	68	41	14
3	27	6	9	14	9	2
4	25	3	4	4	3	1
5	23	3	2	1	1	0
6	28	3	2	0	0	0
7	17	2	1	1	0	0
8	20	0	0	0	0	0
Per cent in upper cm	9	47	65	78	85	92

at Lake Michigan had comparatively large numbers in the deeper samples with only 9 per cent of all specimens in the top centimeter of sand. N. Trout was intermediate with 65 per cent in the top centimeter and Day was at the other extreme with 92 per cent in the top centimeter and no rotifers below a depth of 4 cm. To some extent these differences are governed by exposure to wave action, amount of organic matter in the sand, and the inhabitable width of the beach.

COPEPODA

Although copepods are known to inhabit many unusual environments, it has been

Copepoda in three different beaches, including N. Trout beach with a large population, S. Trout with an intermediate population, and Day with a small population. In comparison with other groups the copepods within a single beach show the least numerical variation over a period of time. The differences from beach to beach, however, were considerable, with some beaches having large numbers (over 200 specimens in some samples) and others having very few. Only the beach studied at Lake Michigan contained no copepods.

In spite of the fact that we have little information concerning the environmental factors which govern the distribution of

TABLE V

DISTRIBUTION OF COPEPODA IN THREE SERIES OF 10 CC SAND SAMPLES. SPECIMENS PER SAMPLE.

Beach and date	Depth of sample, cm	Distance from edge of water, cm							
		0	50	100	150	200	250	300	350
N. Trout Aug. 1, 1937	1		1	9	108	121	49	2	
	2	2		23	113	277	119	2	
	3	1		2	74	196	25	35	2
	4		2		30	189	15	37	
	5	1	5		35	9	2	24	1
	6		5		12	78		23	
	7		12		32	4	1	10	
	8		4		5	4			
		0	60	120	160	200	240	280	
S. Trout Aug. 18, 1936	1		4			36	26	6	
	2		1		9	35	8	2	
	3		4		1	22	3		
	4				1	18	10		
	5					9	4		
	6					2			
	7								
	8								
		0	50	100	150	200	250		
Day July 7, 1937	1					2			
	2					12	3		
	3					22	1		
	4					11	7		
	5					2			
	6						1		
	7								
	8								

Copepoda in the various beaches, we believe that the most important element is the amount of interstitial water. In general, the greatest numbers of Copepoda were found in the middle portions of the beaches where the sand is neither saturated nor too dry. This response to an optimum amount of water is shown in Fig. 8. In beaches having gradual slopes the largest numbers of copepods were found at some distance from the edge of the water (200 to 300 cm), but in beaches having steep slopes the larger numbers were found from 100 to 200 cm from the edge of the water. No copepods, except a few planktonic *Cyclops*, were found in the submerged sand near the shore.

Calculations of the mean vertical distribution of the copepods (Table VI) showed a variety of conditions. At the narrow

Boulder and W. Crystal beaches, for example, few copepods were found and nearly all of these were in the top 4 cm of sand. S. Trout, E. Crystal, and Starrett beaches showed well-defined gradients with a comparatively large population in the top centimeter of sand and less than one specimen per sample in the eighth centimeter from the top. At N. Trout the mean population in the surface samples was 20.7 specimens per 10 cc sand sample while the bottom centimeter contained 7.4. At White Sand (a comparatively flat beach) the usual type of distribution was reversed, with less than one in the surface sample and 8.1 in the bottom centimeter. This condition was due to the fact that many copepods were found in the deeper layers of sand at 300 and 350 cm from the edge of the water where the surface of the sand was quite dry. Con-

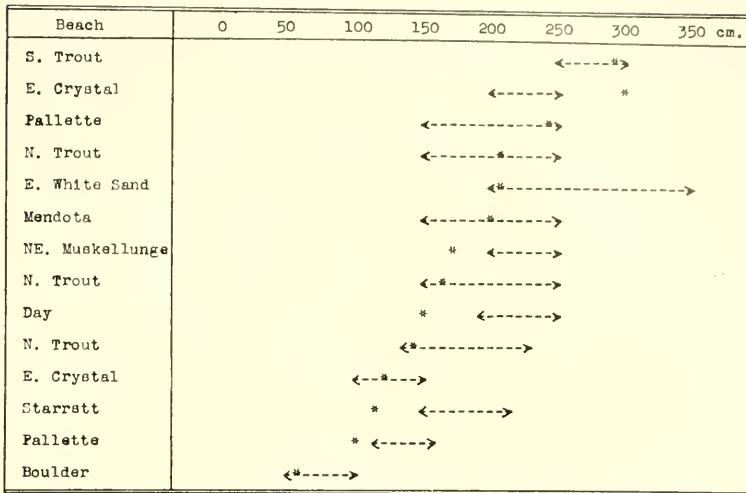


FIG. 8. Horizontal distribution of maximum numbers of copepods in 14 different series of sand samples. Asterisks indicate points on surface of sand which were 12 cm above lake level.

siderable numbers of Copepoda were also found in the deep samples at beaches exposed to frequent and vigorous wave action. In several instances these organisms were found as deep as 11 cm.

OTHER ORGANISMS

Insect larvae, particularly Diptera, were found distributed at random in the beaches. Although a few were as deep as 7 cm, most were in the upper 4 cm. They were numerous in beaches containing large quantities of organic material and in several instances numbered more than two individuals per 10 cc of sand.

Gastrotricha were present in most of the samples taken within 150 cm of the lake

where the sand was quite wet. Some samples contained more than 100 individuals, but in most cases there were comparatively few.

Nematodes were abundant in the outer regions of beaches. Some series of samples had mean populations of more than 2 per 10 cc of sand.

Turbellaria of the genus *Dalyellia* were numerous in certain beaches, up to 15 per sample. The majority by far were found within 150 cm of the shoreline.

Many species of algae inhabit the sand; the main groups are the Cyanophyceae, Chlorophyceae, and Bacillariae of the genera commonly found in the plankton. On the shores of soft-water lakes desmids were

TABLE VI

MEAN VERTICAL DISTRIBUTION OF COPEPODA TO A DEPTH OF EIGHT CM IN SEVEN DIFFERENT BEACHES. MEAN NUMBERS OF SPECIMENS PER 10 CC SAND SAMPLE.

Depth, cm	Beach						
	Boulder	W. Crystal	Starrett	E. Crystal	N. Trout	S. Trout	White Sand
1	0.8	2.4	17.6	11.1	20.7	6.4	0.7
2	0.6	1.0	21.0	7.8	30.8	4.8	0.7
3	0.9	0.8	24.6	8.8	20.0	3.0	1.0
4	0.6	0.8	13.0	7.3	18.7	3.6	2.0
5	0.1	0.3	8.6	2.5	7.4	2.8	2.3
6	0.0	0.0	4.0	1.6	6.5	2.1	2.5
7	0.0	0.0	0.8	0.8	6.6	1.2	3.5
8	0.0	0.0	0.0	0.2	7.4	0.3	8.1

abundant and in hard-water lake beaches great concentrations of diatoms were found as far back as 250 cm from the edge of the water. Needless to say, the psammolittoral presents many interesting problems for the algologist.

Except in the early spring, the remains of zooplankton organisms such as *Cyclops*, *Diaptomus*, *Keratella*, and *Polyarthra* were negligible.

In conclusion we make this statement: If an "average" 10 cc sand sample be taken from the surface of a beach at a distance of

150 cm from the edge of the water, it will be found to contain 4,000,000 bacteria, 8,000 Protozoa, 400 Rotatoria, 40 Copepoda, 20 Tardigrada, and small numbers of other microscopic Metazoa. The sample will be found to contain from 2 to 3 cc of water. In this small volume of water, then, is concentrated a great population, finding all conditions necessary for a flourishing existence. So far as the author has been able to discover, there is no other environment which is capable of supporting such a diversified and dense population of microscopic organisms.

ROOTED AQUATIC PLANTS AND THEIR RELATION TO THE LIMNOLOGY OF FRESH- WATER LAKES

By L. R. WILSON

COE COLLEGE, CEDAR RAPIDS, IOWA

THE ROOTED AQUATIC PLANTS AS A BIOLOGICAL GROUP

If we examine the rooted hydrophytes as a biological group, we are impressed by the fact that they come from practically all parts of the vascular plant kingdom. The Pteridophytes contribute members from the genera *Equisetum*, *Isoetes*, and the water ferns. The monocotyledons which contribute great numbers of species are from the genera *Typha*, *Sparganium*, *Potamogeton*, *Zostera*, *Najas*, *Juncus*, *Sagittaria*, *Alisma*, *Elodea*, *Anacharis*, and *Vallisneria*, as well as some grasses and sedges. The dicotyledons are represented by such families as the Buckwheat, Hornwort, Water Lily, Crowfoot, Waterwort, Evening Primrose, Water Milfoil, Parsley, Primrose, Convolvulus, Figwort, Bladderwort, Lobelia, and Composite.

Such an assemblage of families and genera from all parts of the vascular plant kingdom, except from the Gymnosperms, raises the question of origin for these hydrophytes. It is sufficient to state here that there is reason to believe that the Angiosperms, at least, were originally terrestrial and that some members have become semi-aquatic or entirely aquatic.

The close relationship between the anatomy of the hydrophytes and the waters in which they live is not only of prime importance to the plants in question, but is also important to those smaller plants and animals which depend upon them for support, protection, or food. Probably the most important modification in their anatomy is the development of spongy tissues called aërenchyma. These tissues provide air spaces in the various parts of the plants, and serve in various capacities in their physiology, and in the life histories of the

invertebrates which live upon them. Most of these plants are perennial, and coupled with their more or less uniform environment, tend to produce somewhat permanent communities of plants and associated animals. Therefore, a more static ecology is likely to exist in water than on land.

THE GEOLOGIC AND PHYSIO-CHEMICAL FACTORS

It is common knowledge that the geology of any particular region determines the soils and the characteristics of lakes which are formed in it. The soils which have evolved from the bedrock, or from the materials that have been variously transported to a particular region and modified by climate, determine to a large extent the vegetation of the region. This statement applies to both the vegetation of the land and of the water.

The relationship of bedrock to lake chemistry appears to be well illustrated in Wisconsin. An examination of the geological map of that state shows a large area in the southern part to be covered by limestones, while in the northern part there is a smaller area where granites are exposed. It may be generally stated that the lake waters upon the limestones are harder than those upon the granites. This difference of lake waters may also be a direct reflection of the glacial drifts in regions where the bed rocks are deeply buried. In regions, as in north central Wisconsin, where the glacial drift is derived largely from acid rocks, the lake waters are softer than in regions where the drift is derived from limestone. Lakes that were formed by some geologic agent which left the bed or basin developed on solid rock, or with little or no fine elastic material, show different physical and chemical characteristics than those that

have resulted from geologic agents that have caused the deposition of the finer sediments. In those regions of glacial scour the former type of lake is common, and the vegetation in these lakes is usually very scarce. In regions of glacial dissipation the lake basins are usually constructed of drift materials. Here the vegetation is much more abundant. This also may be true of lakes of non-glacial origin that possess finer sediments.

It has been aptly stated that a lake begins to die immediately after it is born. Thus sedimentation enters into the development of lakes, and determines the soils, the color of the water, the abundance of electrolytes, the hydrogen-ion concentration, and the quality and quantity of the vegetation in them.

The diagram below is suggested as an example of lake development and the accompanying physio-chemical changes. This scheme is the result of observations on more than 200 lakes in northern Wisconsin, and a complete discussion is shortly to be published.

CLASSIFICATION OF LAKES WITH RESPECT TO THE ROOTED HYDROPHYTES

To construct an entirely satisfactory classification of lakes, that can be widely applied with respect to the rooted hydrophytes, is very difficult and probably should not be attempted until much more work is completed. There are possible classifications that consider one or more factors such as origin, structure, geography, and morphology, but it is soon apparent in nature that many of these factors occur in combinations which make it difficult to compare lakes of one region with another without involving elaborate descriptions.

A classification of use to workers in aquatic plant ecology must consider the dynamic factors of lake development, and these must be well enough understood to enable one to trace them from one lake to another, and from one region to another, in order that the dynamic nature of aquatic plants may be determined. These factors are closely related, and the part played by

the plants in the sedimentation of lakes is an important one. When a large number of lakes are examined they show properties that characterize them as one type of lake or another, for example clear water, sandy soils, and sparse vegetation, or turbid water rich in phytoplankton and rooted hydrophytes, or brown water, organic soils, and little vegetation. These lake types have received the names oligotrophic, eutrophic, and dystrophic, respectively, and they serve well in rough descriptive work on the rooted aquatic plants. This classification, however, does not give a complete representation of the dynamics of plant ecology for any one locality, much less for widely separated regions. Within regions where hundreds of lakes are present one encounters many intermediate types, and parts of large lakes may belong to all three types. The very fact that all three types may occur in a single lake is indicative of lake development, and the use of these terms is very convenient in describing the character of a lake or portion of it.

Pearsall (1920, 1921, 1929) in several papers has used the terms "primitive" and "evolved" lakes, and has shown that the vegetation is distinctive in each. He further shows that they are dynamic in their development and that evolved lakes have developed from primitive lakes by silting.

The Wisconsin Geological and Natural History Survey has for a number of years used the terms *drainage* and *seepage* in describing the lakes of Wisconsin. This classification though incomplete in its morphological description appears to have the advantage in that many physical, chemical, faunal, and floral characteristics can be predicted for lakes when information pertaining to the drainage system is known. For example, a lake belonging to a drainage system is often eutrophic in character, while a seepage lake in Wisconsin is seldom of this type, but usually oligotrophic, or dystrophic in character. The seepage lakes of Wisconsin, and the Middle West in general, are located in kettle holes of pitted outwash plains, or in moraines. They have

no apparent drainage into them other than that which enters by surface drainage from the edges of their particular kettles, or from meteoric sources. No outlet is present except on rare occasions of high water. It appears that the drainage lakes receive a constant addition of mineral salts from their inflowing streams and tend to have harder water than the seepage lakes. Chemical examinations have confirmed this. The writer used this classification in a study of the flora and its quantity in the lakes of northern Wisconsin, but it soon became apparent that a further division of the classification was needed. Having, apparently, a natural division of lakes to begin with, the most desirable things to know concerning these lakes, then, were the stages through which they passed in their morphology. Hydrographic characters were determined and the lakes were divided into *youthful*, *mature*, and *old age* stages, after the common practice of geologists. This scheme is outlined in Fig. 1. When ap-

plied to ecological studies of the plants the proposed scheme of lake development and classification was found to be very useful. Lakes fitting specific descriptions were found to have certain assemblages of plant species, and conversely when a lake flora was listed by another worker it was found possible to predict, with almost certainty, the place occupied by the lake in the classification. The scheme outlined in Fig. 1 is suggested only for northern Wisconsin, and it will probably need modification or revision if applied to other regions. It is very clear that before any classification of lakes can be widely used in this country for the rooted aquatic plants, a more intensive survey of the lakes of North America must be made.

THE HARDNESS AND ALKALINITY OF LAKE WATERS

The factors of hardness and alkalinity have been widely used in studying the distribution of aquatic plants. Probably the

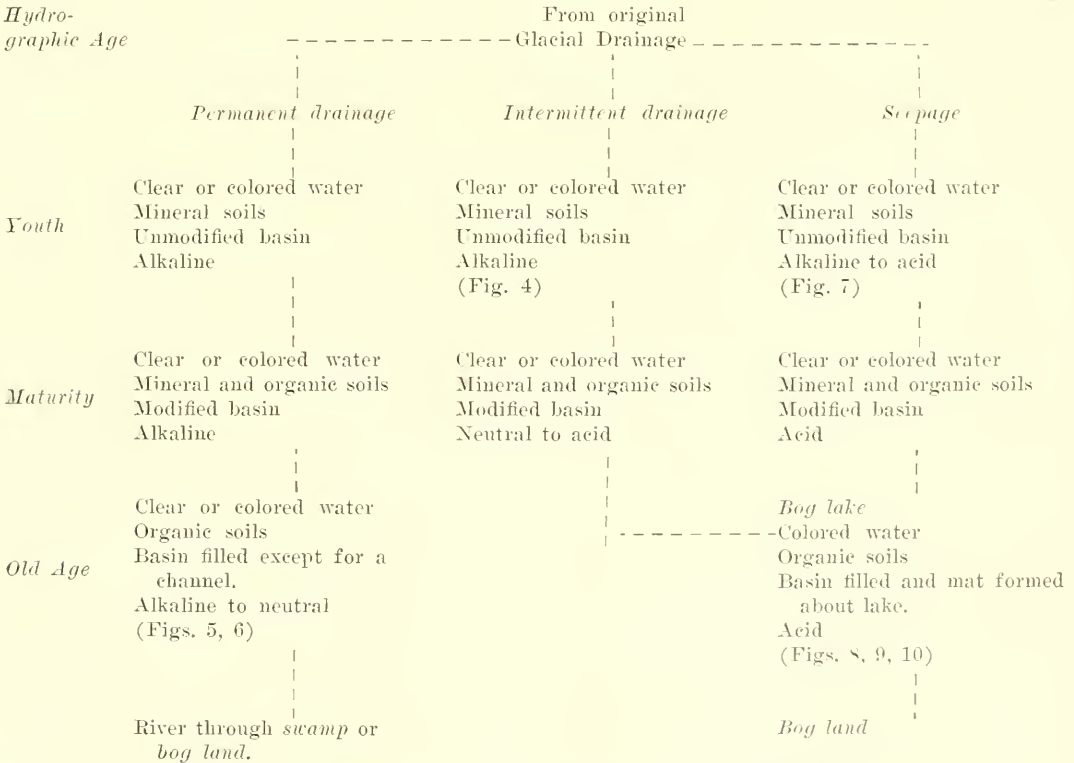


FIG. 1. Diagram of lake development in Northern Wisconsin.

most extensive use of these factors has been made by Steenis (1932, 1933, 1934, 1935). Several hundred lakes were investigated by him in a survey of the economic value of the larger aquatic plants to fish, game, and summer resorts in Wisconsin. The tables presented in Steenis' papers show conclusively that a marked correlation exists between the vegetation and soft, medium hard, and hard waters. Additional work by the writer on more than 100 lakes in adjoining territory agrees with the findings of Steenis. The classification of waters that was used in these studies is one that has been employed for a number of years by the Wisconsin Geological and Natural History Survey, and is given below:

Soft—	0-10 parts per million of bound carbon dioxide.
Medium—	10-30 parts per million of bound carbon dioxide.
Hard—	over 30 parts per million of bound carbon dioxide.
	Gray-green.
	Soft or fluid.

Steenis has followed and extended an ecological classification of the hydrophytes begun by Fassett (1930). This classification is similar to Warming's (1925) "growth forms" and for practical value in classifying the lakes of Wisconsin it is very useful. It is not without the fault, however, of being somewhat empirical. When a study is made of Steenis' charts it is evident that the "growth forms" of the aquatic plants overlap several of his lake types, and when viewed in their entire distribution they merge into a complicated pattern of dynamic succession.

^ A study of the vegetation in 102 lakes of northern Wisconsin for its relation to the pH of the waters has been made by the writer, and the greatest number of species was found in those lakes having slightly more than the pH of 7.0. An examination of the plant species showed them to be inhabitants of either acid or alkaline waters and a few that grow in both environments. Therefore, the greatest number of species appears to occur where the first two overlap in their tolerance range.

LIGHT

The necessity of light for the growth of aquatic plants is probably one of the most important factors in vertical distribution. The number of published studies dealing with the relation of light to aquatic plant distribution is very few, and all show the need for further intense work in this field. Pearsall (1920, 1933, 1934) working with the iodide-sulphuric acid method in the lakes of the Windermere District of England has shown the lower limit of vegetation growth to be at approximately the depth of 2 per cent of full daylight. In 1920 this was at 6.5 meters while in 1932, due to the change in the transparency of the water, caused by the greater abundance of phytoplankton, the lower limit of rooted vegetation was 4.3 meters.

Juday (1934), using a photoelectric method, records the occurrence of two species of mosses and one species of hepaticae growing at depths of 18 to 20 meters in Crystal Lake, Vilas County, Wisconsin. At 18 meters, only one to 4 per cent of the solar energy penetrates at midday.

Wilson (1935), also using photoelectric observations, studied the vertical distribution of vegetation in three Vilas County, Wisconsin, lakes and found that the maximum vegetation limit was reached at the depths where approximately 4 per cent of total sunlight penetrated. This was found to vary from 7 meters in Muskellunge Lake to 3 meters in Little John Lake. The latter lake possessed an abundant crop of phytoplankton, which made the water very turbid.

TEMPERATURE

The affect of moderately low temperatures upon the rooted aquatics does not appear to be one of the very important ecological factors in their ultimate growth and distribution. This is probably because the vertical distribution of the rooted plants generally does not extend to depths where the waters are very cold. They appear to be restricted in this distribution, by the scarcity of sunlight, long before the low temperatures of the lake waters are reached.

In lakes of the Rocky Mountains that are fed by glaciers or snow fields, the vegetation is usually absent or very scarce. Here the extremely cold water may be a factor in the absence or restriction of the rooted hydrophytes similar to the observations of Magnin (1893). It is also true that these lakes are rocky and could support but few plants, or they are rapidly silting with rock flour, which equally prevents plant growth.

The same retarding effect of latitude, that is evident upon land vegetation, is also observed in aquatic plant communities. The aquatic vegetation of the higher latitudes is seasonally slower in its development than that of the lower latitudes.

When the first cooling of the lake water is observed in the autumn a sharp change takes place in the aquatic vegetation. It quickly loses its thrifty appearance, and before the fall turnover of the lake water is well under way, most of the vegetation has disappeared or rotted. As far as the writer is aware, no extensive study has been made of the relation of temperature to the growth of aquatic plants.

SOILS

The importance of soils in the ecology of rooted aquatic plants is now thoroughly appreciated. Pond (1905), Brown (1911), Veatch (1933), and Wilson (1935, 1937) in this country and Pearsall (1920, 1921, 1923, 1925, 1929) in England have demonstrated the importance of soils in the physiology of the aquatic plant, or in the development of hydrophyte communities.

Pond (1905) and Brown (1911) demonstrated, after experimenting with numerous aquatic genera possessing roots, that they grew better if rooted in soil than if suspended over it, or rooted in clean washed sand.

Pearsall and Pearsall (1923) found that the leaf-shapes of *Potamogeton perfoliatus* and *P. praelongus* varied sufficiently on different soils to suggest that the proportion of lime in the soils is an important factor in determining the leafshape of these species, and that varieties in *P. perfoliatus* are only growth forms. Pearsall and Hanby

(1925) further investigated the variation of leaf form in *P. perfoliatus* and concluded that the extreme variability of leaf form is due to the variations under natural conditions of (1) the light intensity and duration, (2) the calcium content of the soil, and (3) the ratio of potassium (and monovalent ions generally ?) to calcium in the soil if little calcium is present.

Veatch (1931, 1933), working in the state of Michigan, studied the subaqueous soils. He proposed a classification of these and made observations on some relationships between water plants and the water soils.

Below, only the portion of Veatch's classification of water soils that is applicable to fresh-water lakes is given.

I. Lacustrine group.

AI. Shallow aqueous horizon (tentatively restricted to less than 10 feet).

A. Calcic water.

1. High calcic or hard water (14+ grains per gallon hardness).

a. Sand subaqueous horizon.

Clean sand compact.

Sand-organic matter admixed.

Sand-shells or marl admixed.

b. Clay-colloid subaqueous horizon (largely inorganic).

Dark colored muds.

Gray-green muds.

Reddish muds.

c. Slime or ooze (largely organic and gelatinous or pasty in consistency).

Black or brown.

Gray-green.

d. Peat subaqueous horizon.

Soft or fluid.

Compact or matted.

e. Marl subaqueous horizon.

Soft or oozy.

Compact.

Nodular or pebbly.

f. Gravel-boulder bottom.

g. Hard rock bottom.

2. Medium calcic water (6 to 13 grains per gallon hardness).

(Subdivisions same as under high calcic waters.)

3. Low calcic and soft or acid water (6 grains per gallon hardness).

(Subdivisions as above except 'e'.)

The general conclusions at which Veatch arrived after visiting about 300 widely distributed localities in Michigan are the fol-

lowing. The least growth of rooted aquatic plants is upon nearly pure sand, cobbles, and hard rock, while the most prolific growth is upon the soft slimy sedimentary peat, or organic mud, or upon the soft, silty, or clayey inorganic muds.

The genus *Potamogeton* is most abundant in calcareous and alkaline waters and on the soft or fluid organic "mud," and on the soft marl. Some species, however, were observed on all types of bottom except indurated rock. One species occurs in soft or slightly acid water.

Nymphaeanthus and *Castalia* appeared to be most abundant in soft, fluid, organic mud. The waters ranged from very soft to hard.

Scirpus validus, and possibly related species are common on "hard" bottoms, except bedrock. The waters ranged from acid to alkaline.

Zizania aquatica grows in clear water with a range of hardness of 6 to 17 grains per gallon, and a pH of 8.0 to 8.6. The soils were soft, fluid, organic mud, or peat, thin peaty mud over calcareous clay, and clayey inorganic calcareous mud.

Sagittaria and *Pontedaria* are most abundant in shallow alkaline or hard water over the more clayey (inorganic) mud or in peaty sands. A few were recorded on acid peats.

Typha latifolia is most abundant on the more clayey muds and on a thin covering of black alkaline organic soil over clay or calcareous sand and silt. The associated waters were alkaline. A few plants were observed on coarse acid peat.

Eriocaulon septangulare grows over either peat, peaty sand, or clean non-calcareous sand. This plant appeared to be a very reliable indicator of soft, and nearly neutral or slightly acid water.

Pearsall (1920, 1921) and Wilson (1935, 1937) have shown that there are important relationships between the sedimentation of soils and the succession of the rooted aquatic plants, but this will be discussed under the heading of dynamic ecology.

DYNAMIC ECOLOGY

The fact that plant formations are not

static features has been known a long time. That they evolve along certain trends is observable wherever plants grow. The aquatic plant communities are no exception, but attempts have been made to classify them in such a way that may lead one to suspect that they are static. Pearsall (1918) has discussed the classification of aquatic plant communities and has shown that one must consider them as stages or steps in a single development reaching from the early stages of lake colonization to the closed swamp or moor. These stages go hand in hand with sedimentation.

The dynamic factors affecting aquatic vegetation in the English lakes have been set forth in papers by Pearsall (1921, 1929), and these may be generally applied to the lakes of this country. He states that two sets of factors which govern the development of aquatic vegetation are (1) those affecting the lake as a whole, and (2) the forces altering the shore.

Pearsall (1920) found that where silting is rapid the soils are richer in available potash and usually in phosphates and nitrates. Also they are more abundant in the finer silts. He, therefore, assumes that the variation in the quality and quantity of silts very largely controls the distribution of submerged vegetation. Figs. 2 and 3 (Pearsall 1921) show diagrammatically the aquatic vegetation associated with the quality and quantity of sediments in shallow and deep water in the English lakes.

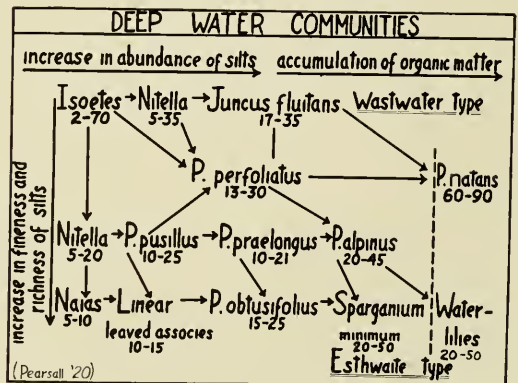


FIG. 2. Diagram of plant succession among communities of plants below the zone of erosion. The figures given indicate the percentage of organic content of the soil.



FIG. 5. Rice Lake near Boulder Junction, Vilas County, Wis. A drainage lake in an old age stage of development. The lake basin is nearly filled with organic soils, and the vegetation is very abundant. See also Fig. 6.



FIG. 6. Rice Lake near Boulder Junction, Vilas County, Wis. The lake is almost filled with sediments and aquatic vegetation, and only a channel remains through the wild rice and bordering swamp land.



FIG. 7. Crystal Lake, Vilas County, Wis. A clear, soft-water lake of the seepage type in a youthful stage of development and an example of a lake possessing a flora of the "rosette" type.



FIG. 8. Midge Lake, Vilas County, Wis. A young bog lake in which the shrubs, *Andromeda*, *Chamaedaphne*, and *Alnus* have invaded the littoral soils and replaced *Eriocaulon*, *Gratiola*, and *Utricularia resupinata*. These latter are now members of the lake flora. See also Fig. 9.



FIG. 9. A community of *Eriocaulon*, *Potamogeton*, *Sparganium*, and *Castalia* in a young bog lake. Here the littoral vegetation, represented by *Eriocaulon* and *Gratiola aurea*, f. *pusillus* (submerged) has been displaced from the subaërial soils by invading shrubs. They remain a member of the lake flora because the water is still shallow near the shore. Midge Lake, Vilas County, Wis. See also Fig. 8.



FIG. 10. An old bog lake nearing closure. The only remaining aquatic vegetation is *Nymphaeanthus variegatus*. Vilas County, Wis.

A study of the tables published by Fasset and by Steenis show that species of the first type are most abundant in those lakes of medium hard, or hard water. Species of the second type are most abundant

in the soft clear water lakes and in bog lakes. Species of the third type may occur in all fresh waters. Species of the fourth type occur almost exclusively in the medium and hard-water lakes. The spe-

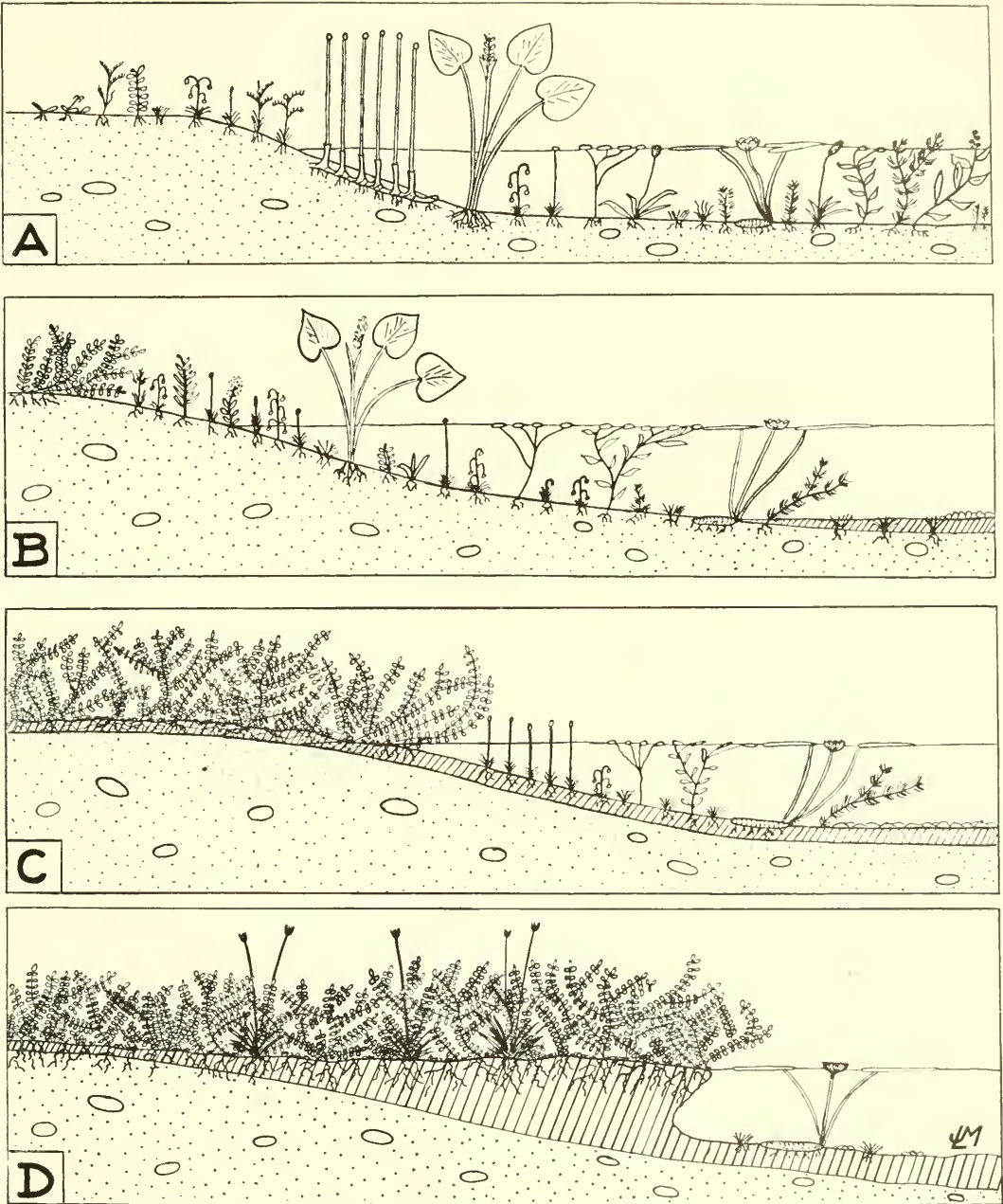


FIG. 11. Diagrams showing stages in the succession of aquatic plants in seepage lakes of Northern Wisconsin. See text for discussion.

cies of the fifth type are like the fourth in their distribution.

It appears then that the habitat is reflected in the vegetation and an understanding of the relationships which exist between the lake, the vegetation, and the animal life in the lake is of great value to the applied scientist. Here in the "growth forms" there appears to exist a rough index to the productivity of a lake. From the above, an inference may be made pointing to a static nature of the aquatic plant community. When observed more closely, and with reference to the hydrographic age and drainage of the lakes in which these types grow the dynamic quality is very obvious.

It will be noted that all five "growth forms" occur in medium hard-water lakes, and reference to Fig. 1 shows that these are either drainage lakes or seepage lakes in youth. This luxuriant vegetation is diagrammatically shown in A of Fig. 11. All "growth forms" occur here, and in the succeeding diagrams B, C, and D it is indicated how, by development, the seepage lakes lose species belonging to types one, four, and five. Types two and three persist longer, but eventually only type three, which has floating leaves and horizontal stems, is found to live in the lakes, as they near old age and extinction. A fuller discussion of these problems of the Wisconsin lakes will be published.

On page 119 is a diagram of the aquatic succession in Muskellunge Lake in Vilas County, Wisconsin. This lake is typical of the region and might be considered in early maturity and of the intermittent drainage type. The diagram summarizes the relationships which exist among the various aquatic communities, and shows how they are related to the substratum.

PRODUCTIVITY STUDIES

In 1926 Klugh suggested that the abundance of the larger and rooted hydrophytes might be taken as an index for the productivity of lakes. He cited attempts at determining such an index for lakes, and suggested that upon investigation the hydro-

phytes might prove to be the simplest and most useful method of determining the productivity of a lake in terms of fish.

Many rough observations have been made upon the abundance of certain species of aquatic plants, and upon the entire crop in lakes. These have value in that they allow general statements to be made concerning the relative abundance of the vegetation, but more exact studies should be undertaken.

The number of published studies that have been made with reference to the weight of the total crop of rooted hydrophytes are very few and entirely inadequate for any reliable correlations with the density of the fish population, or with other factors. In this country published studies have been made in only five lakes, all of which are in Wisconsin (Rickett 1922, 1924; Wilson 1935, 1937). In each, sample quadrates were studied along profiles in various habitats. The plants were removed from the quadrates and separated into species. Dry weights were determined, and the entire crop in the lake was estimated from these samples.

A comparison of the estimations is most interesting, for it shows how varied the quantity of aquatic plants may be in different regions. The work of Rickett was done in Southern Wisconsin and that of the writer, in Northern Wisconsin.

Region	Total crop (kilograms)	Average crop per sq m (grams)
Southern Wisconsin		
Lake Mendota	2,100,000	202
Green Lake	1,527,900	178
Northern Wisconsin		
Little John Lake	111	.52
Muskellunge Lake	882	.45
Silver Lake	17	.08

The explanation for the great difference in the abundance of the aquatic plants in the two regions appears to be the following: (1) sandy soils predominate in the north, while silt and clay are more abundant in the southern lakes, (2) there is

SUMMARY OF PLANT COMMUNITIES IN MUSKELLUNGE LAKE, A PRIMITIVE LAKE

ZONE I (0-1 m)	ZONE II (1-3 m)	ZONE III (3-8 m)
rocks, sand, silt (unleached)	rocks, sand, silt (unleached)	sand, silt (unleached)
<i>Bidens Beckii</i>	<i>Bidens</i>	<i>Chara</i>
<i>Castalia odorata</i>	<i>Chara</i> sp.	<i>Najas</i> (flexuous form)
<i>Chara</i> sp.	<i>Isoetes</i>	<i>Nitella</i> sp.
<i>Elodea acicularis</i>	<i>Myriophyllum</i>	<i>Nostoc</i> sp.
<i>E. palustris</i>		
<i>Equisetum limosum</i>	<i>alterniflorum</i> -----	<i>Potamogeton amplifolius</i>
<i>Isoetes macrospora</i> -----	<i>M. tenellum</i>	<i>P. gramineus</i> , var.
<i>Myriophyllum alterniflorum</i>	<i>Najas</i> (intermediate form)	<i>graminifolius</i>
<i>M. tenellum</i>	<i>Nitella</i> sp.	<i>P. pusillus</i>
<i>Najas flexilis</i> (bushy form)	<i>Nostoc</i> sp.	<i>P. Robbinsii</i>
<i>Nymphozanthus variegatus</i>	<i>Nymphozanthus</i>	
<i>Polygonum natans</i> , f. <i>genuinum</i>	<i>Potamogeton amplifolius</i>	organic soil (well decomposed)
<i>Potamogeton gramineus</i> , var.	<i>P. epiphydrus</i>	<i>Najas</i>
<i>graminifolius</i>	<i>P. gramineus</i> , var. <i>graminifolius</i>	<i>Nitella</i> sp.
<i>P. natans</i>	<i>P. praelongus</i>	<i>Nostoc</i> sp.
<i>P. Spirillus</i>	<i>P. pusillus</i>	<i>Potamogeton amplifolius</i>
<i>Sagittaria gramineus</i>	<i>P. Robbinsii</i>	<i>P. pusillus</i>
<i>Scirpus acutus</i>	<i>P. Spirillus</i>	<i>P. Robbinsii</i>
<i>Vallisneria americana</i>	<i>Vallisneria</i>	
sand, silt (leached)	organic soil (well decomposed)-----	
<i>Castalia</i>	<i>Bidens</i>	
<i>Elatine minima</i>	<i>Castalia</i>	
<i>Elodea acicularis</i>	<i>Chara</i> sp.	
<i>Eriocaulon septangulare</i>	<i>Elatine</i>	
<i>Gratiola aurea</i> , f. <i>pusilla</i>	<i>Elodea acicularis</i>	
<i>Isoetes</i>	<i>Isoetes</i>	
<i>Juncus pelocarpus</i> , f. <i>submersus</i> --	<i>Myriophyllum alterniflorum</i>	
<i>Littorella americana</i>	<i>Najas</i>	
<i>Lobelia Dortmanna</i>	<i>Nitella</i> sp.	
<i>Myriophyllum tenellum</i>	<i>Nostoc</i> sp.	
<i>Nymphozanthus</i>	<i>Nymphozanthus</i>	
<i>Ranunculus reptans</i> , var. <i>ovalis</i>	<i>Nymphozanthus</i>	
<i>Sparganium angustifolium</i>	<i>Polygonum</i>	
	<i>Potamogeton amplifolius</i>	
	<i>P. epiphydrus</i>	
organic soil (partly decomposed)	<i>P. gramineus</i> , var. <i>graminifolius</i>	
<i>Castalia</i>	<i>P. praelongus</i>	
<i>Elatine</i>	<i>P. pusillus</i>	
<i>Eriocaulon</i>	<i>P. Robbinsii</i>	
<i>Elodea acicularis</i>	<i>Vallisneria</i>	
<i>Gratiola</i>		
<i>Isoetes</i> -----		
<i>Juncus</i>		
<i>Littorella</i>		
<i>Lobelia</i>		
<i>Nymphozanthus</i>		
<i>P. natans</i>		
<i>Sparganium</i>		
organic soil (fibrous, "raw")		
<i>Castalia</i>		
<i>Eriocaulon</i>		
<i>Nymphozanthus</i>		
<i>P. natans</i>		
<i>Sparganium</i>		
Swamp and bog		

greater bulk of tissue in the dominant species of the southern lakes, and (3) there are also greater areas of lake bottom covered by the plants in these lakes.

ECONOMIC CONSIDERATIONS

Reighard (1915), Baker (1918), Muttowski (1918), C. B. Wilson (1924), and others have shown that the presence of rooted aquatic plants is very important in lakes and ponds where aquatic animals are to thrive. To the invertebrates the vegetation serves not only as "cover," but also as a source of food. The larger animals are feeders upon the invertebrates and consequently indirectly depend upon the plants for food.

Reighard (1915) discussing the distribution of fishes in the Douglas Lake region of Michigan shows that three species are found in the neighborhood of stony shoals, five species frequent the deep waters, and that ten species are found associated with the submerged vegetation.

Muttowski (1918) observed in Lake Mendota that in the bottom areas populated by plants the fauna was more abundant and varied than elsewhere.

Discussing the submerged vegetation of Oneida Lake, Baker (1918) states that the greatest development of plant and animal life is within the six-foot contour. He points out that each plant is important to the lives of a host of animals, the primary food of which is such plants.

The part played by the emersed aquatic vegetation in the biology of certain invertebrates has been studied by Frohne (1938). The number of species of insects he found living upon these plants is shown below:

PLANTS	SPECIES OF INSECTS
1. <i>Scirpus occidentalis</i>	24
2. <i>S. validus</i>	9
3. <i>S. americanus</i>	10
4. <i>Eleocharis palustris</i> , var. <i>major</i>	9
5. <i>Carex vesicaria</i>	10
6. <i>Phragmites communis</i>	6

Pearsall (1921, 1929) discussing the vegetation in the lakes of England has stated that there is a correlation between

the hydrographic age of lakes, and the vegetation of lakes; also, a correlation exists with the fish life. This is shown in the following chart.

	Primitive	Evolved
Physical type	Rocky	Silted
Submerged and rooted vegetation	Isoetes and Nitella	More Potamogeton spp. with Naias, Elodea, etc.
Phytoplankton	Green algae, desmids and often d y n o - bryon	Chiefly diatoms with more blue green algae
Fauna	C h i e f l y trout	Pike and Perch abundant

A somewhat similar chart has been constructed for the lakes of Wisconsin. In this is shown the characteristic vegetation in lakes of certain physical and chemical description, and the types of fish most abundant in them. Should this chart prove correct upon further investigation, it might serve as a help to the stocking of lakes with game fish.

Lake	Plants	Fish
Water medium to hard, mineral or organic soils	Lax stems, compound or flexuous leaves	Muskel-lunge, pickerel, pike, bass, etc.
Soft-water mineral soils	Short unbranched stems, leaves stiff, or in rosettes	Perch and bass
Soft-water bog lakes	Stem horizontal leaves floating on surface	Bass or none

Aquatic vegetation is not only important to those animals which spend all or part of their life histories below the water, but also to many of the larger vertebrates. Of these, ducks, fur bearing animals, and large game are the most important. These animals are

often specific in their choice of aquatic plants for food and shelter and an understanding of the ecology of such plants is of prime importance in order to carry out a natural program of conservation (McAtee 1917).

A word may be said concerning the intelligent use of lakes by resort owners. It has been shown that lakes are geologic features that evolve along definite trends. With this evolution goes definite floral and faunal development. It seems then that a lake should be studied and made to serve those ends for which it is best suited. A lake with very soft water, for instance, may never be a good fishing lake, since it lacks in food supply, and it would be a waste of effort to stock it. On the other hand it may become important to a different type of aquatic recreation. Lakes with abundant plant life may be undesirable as bathing and boating lakes, but they may become important to the fisherman by intelligent husbandry.

PROBLEMS REQUIRING INVESTIGATION

1. *Relation of light, temperature, hardness, etc., to aquatic plant distribution.* These environmental studies should be undertaken if possible with controlled conditions. When general rules are arrived at they should be compared with field results.

2. *Relation of sedimentation to the rooted aquatic plant.* The factors of sedimentation and plant succession are closely related as dynamic processes, and in each region, where lakes occur, there is need for careful observations. A fuller understanding of the sediments, their origin, structure, and effect upon the lake waters is needed before a great deal can be accomplished in plant succession. One of the most pertinent problems is a better understanding of the organic sediments.

3. *Histological and Morphological studies.* Much can be accomplished in the field of ecological anatomy and morphology that may explain the distribution and tolerances of aquatic plants. Those species of definite value to fish and game should have further studies made of their reproduction. His-

tological studies should be made in relation to the physiological experiments.

4. *Critical taxonomic studies.* Studies of this nature are important for every region where hydrophytes occur. There should be close correlation between these studies and ecological observations, for there are not only important taxonomic questions to solve, but the presence of certain species, varieties, and forms of rooted hydrophytes within lakes is often indicative of very specific conditions. Taxonomy will become one of the ecologist's most important tools, if use is made of the terms, species, varieties, and forms and there is an understanding of the environments in which they occur.

5. *Productivity studies.* The pursuit of productivity studies is important because they are closely related to the other fields of limnological investigation both scientific and applied.

6. *Relation of aquatic plants to animals.* Many phases present themselves for investigation when the relations of animal life to plants are considered and only a few can be suggested here:

a. The parallel succession of animals and plants.

b. Aquatic plants as food to specific animals.

c. The dispersal of aquatic plants by animals.

d. The role of aquatic plants in the morphology of the invertebrates.

e. Population studies of animals in certain plant communities.

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ROLE OF THE BOTTOM FAUNA IN THE PRODUCTIVITY OF LAKES*

By FRANK E. EGGLETON

DEPARTMENT OF ZOOLOGY AND UNIVERSITY BIOLOGICAL STATION, UNIVERSITY OF MICHIGAN, ANN ARBOR, MICH.

INTRODUCTION

IN the microcosmic economy of a lake, each division of the inanimate habitat, each category of environmental factors, each realm of the biota, forms a structural and functional part of the composite whole. If any one characteristic of lacustrine ecology is more often apparent to the limnologist than any other, it is this interdependency of the physical, chemical, and biological phenomena whose constant interplay weaves a complex design in the fabric of the life of inland waters. The behavior pattern of organisms is everywhere determined by the stimuli which impinge upon them. These stimuli are, in their turn, conditioned by the intrinsic nature of that division of the inanimate habitat within which an organism lives.

Beneath the waters of a lake lies one of the two major categories of lacustrine habitats, the lake floor. There, as elsewhere, the effectiveness with which environmental factors play upon the inhabiting organisms is modified by the particular nature of the immediate environment. Forces inherent in the nature of the substratum itself bend and shape all other forces and thus condition the reactions of the biota. Life in the realm of the benthos is complex, variable, and intricately interwoven with that of the lake as a whole.

Although it is perfectly proper thus to refer to the entire lake floor as one great subdivision of aquatic habitats, it is not to be supposed that there is any marked uniformity of detail in the conditions of existence over the whole basin. Diversity is one of the chief characteristics of fresh-

water situations and the benthic type of habitat is no exception to the general rule. Many of the most potent environmental factors vary markedly with depth and this fact has served as the basis for what is undoubtedly the most widely accepted classification of benthic zones.

Several systems have been proposed at various times but within the last decade the one which has come to enjoy nearly universal acceptance divides the lake floor into three major zones, the littoral, sublittoral, and profundal. A fourth major zone, the abyssal, proposed at an earlier date, has found little favor and less application. This fate seems only natural from the fact that its sponsor proposed to limit it to those great depths, as fresh waters go, below 600 meters. It may be that when the two or three lakes in the world known to have such tremendous depths are more adequately studied we shall have need for the term. Until then the mere fact of depth alone seems insufficient reason for applying it. Unless some significant change can be shown to occur in the benthic habitat or the benthic fauna at that or some other depth there seems small justification for setting off the abyssal from the deeper profundal.

Although limnologists have very generally accepted this terminology for the benthic zones, they have been far less in agreement concerning the exact definitions and limitations of the terms. In 1931 the speaker proposed certain definitions which have enjoyed some degree of acceptance. They were stated as follows:

"... the littoral zone of the bottom is ... that region lying between the shoreline and, approximately, the lakeward limit of (rooted) aquatic vegetation. The

* Contribution from the Department of Zoology and from the Biological Station of the University of Michigan.

profundal zone extends from the greatest depth . . . up the slope toward shore to a level somewhat above that corresponding to the average upper limit of the hypolimnion. The sublittoral lies between these two."

Obviously, under the specifications of these definitions only those lakes which stratify thermally would have a profundal zone and in many shallow, clear-water lakes the whole benthic habitat would lie within the littoral. This is certainly true for temperate lakes of the second and third orders respectively. The conditions which typify the profundal are not established in the warm, shallow, well aerated lakes and second order lakes normally stratify. Temperate lakes of the first order frequently show thermal stratification with true thermocline formation and consequent stagnation. Moreover, except perhaps in the very largest lakes of this order, as for example the Great Lakes of this continent, first order lakes quite typically have very short vernal and autumnal circulation periods and may even exhibit incomplete turnover. These facts and others result in the formation of true profundal conditions beneath the deeper waters of first order lakes and the upper limit of the profundal zone is, in such lakes, approximately coincident with the average upper limit of the hypolimnion when thermal stratification does occur.

The sublittoral is everywhere a transition zone, and being so lacks the positive characteristics of the other major zones. It is really a part of Muttkowski's aphytal zone but is, nevertheless, distinctly differentiated from the true profundal. Muttkowski included it as a subdivision of the littoral under the term "dysphytal." It is, as that writer said (1918), "a region of variable extent, a region of heaping refuse." Within its boundaries, as now understood, may frequently be found a belt-like burial ground for the dead shells from vast molluscan populations in the littoral above. This region is called the shell zone. Lundbeck (1926) found it commonly in the north German lakes. Scott discovered it in some of the Indiana lakes. Muttkowski

described it from Lake Mendota. Miyadi noted its occurrence in certain Japanese lakes. The author has seen it in many small inland lakes and found abundant evidence of its existence along the shelf bounding much of the shoreward waters of Lake Michigan.

Where the sublittoral leaves off the profundal begins. From the very nature of conditions it is to be expected that there should be no sharp line of demarcation between the two. Those forces which establish the conditions typical of the profundal are not static. The level at which the thermocline stands fluctuates with the advance of the season and with other factors within a season. There is thus a region exposed alternately to conditions of the hypolimnion and to those of the thermocline. Moreover, this is the very stratum of the basin wherein the other conditions of the profundal are apt to be blended with those of shallower regions. The bottom deposits, where a sandy littoral merges into a muddy profundal, for instance, shade almost imperceptibly from clean sand through muddy sand and sandy mud into the mud of the lower levels. But to attempt to indicate exactly where the transition ceases, where true profundal first definitely occurs, is both futile and undesirable. Once well within the profundal, however, one discovers a definite combination of circumstances which characterize the area. The temperature is permanently low; pressures are increasing; dissolved oxygen is lacking throughout some part, often much, of the year; hydrogen-ion concentration frequently passes into the acid range; there is little or no light; and very often there is an accumulation of carbon dioxide, methane, and other gases of decomposition.

HISTORICAL RÉSUMÉ

It has often been asserted that limnology, as a separate, organized division of science, is less than half a century old. Some of its subdivisions naturally are younger still. It is true, of course, that certain general facts concerning the organisms which live in and on the bottom of lakes, at least in the more

shallow regions, have long been known. Moreover, Forel and other early workers knew something about a deep-water fauna, although they probably did not realize the existence of a profundal bottom fauna as a group of distinct ecological communities. The equipment available to early limnologists determined the fact that all the pioneer work on benthic organisms was strictly qualitative. It was not until 1911, when Ekman introduced the dredge which now bears his name, that work in this field became quantitative; and until about 1920 one could count all the truly significant studies in this branch of limnology on the fingers of his two hands.

During the latter decades of the last century the early workers in fresh-water biology, employing the methods of oceanography, made some exploratory studies of the deep-water fauna in various lakes both in Europe and in America. Their equipment and methods precluded any possibility of distinguishing clearly between those organisms which lived in the bottom deposit and those which lived in the open water just above it. The concept of a deep-water benthic fauna as a distinct animal association did not emerge, therefore, until after 1900. While Forel was laying the foundations for investigations of bottom fauna in Europe, beginning about 1870, Stimpson, Hoy, Smith, Verrill, and others began publication of the pioneer American work in the same year. During the next 40 years, both in America and in Europe, a rising tide of interest and activity marked the development of limnology generally and as a part of the rest there were scattered studies of deep-water organisms and several investigations which included some qualitative enumerations of true benthic forms. The first decade of the present century saw the publication of the first research which was restricted specifically to bottom fauna. The work of Ekman and the introduction of his dredge in 1911 added a considerable impetus to this phase of limnology. However, before the effect could become conspicuous most of the world became concerned with more compelling but much less profitable

business. Beginning again just after the war, publication has continued at a constantly accelerating rate and during the past 20 years scores of investigators have published literally hundreds of papers on the benthic fauna in at least 15 languages.

Today there are two well-defined aspects of emphasis in limnology generally, and this fact is also quite evident in benthic studies. Fisheries interests, federal bureaus, and the state and regional surveys are accentuating the applied aspect and along with this there is, as always, the basic, fundamental research. Let me hasten to add, that no one need fear exhaustion of the subject because of this activity. To those of us who study in this field it is increasingly apparent that we have only begun to open the way for a tremendous amount of research that needs to be done.

THE BENTHIC FAUNA

When considered from the edge of the water to the greatest depths and in all types of lakes, the benthos comprises representatives from nearly every phylum of animals which occurs in fresh waters at all and from practically all of the larger plant groups. The animals are as diversified morphologically and in habits as they are taxonomically. They vary from those which spend only a small part of their life cycle within the bottom deposits to those which have their whole existence in that habitat. Some are exceedingly active, others are sluggish and sessile. Many build tubes, or cases, or shelters of other sorts, but still more dwell unprotected in the soft mud beneath quiet waters. The situations they choose and the types of substratum which they select range from torrential streams to the stagnant depths of stratified lakes and from flat rocks and great boulders through rubble, gravel, sand, and clay to the soft, semi-flocculent ooze within the profundal zone of many large lakes.

Of the many ways in which it is possible to classify these animals, one of the simplest and most used, although intrinsically artificial, methods is on the basis of size alone. This division has arisen from the practice

of removing the organisms from the substratum by the use of screens and has resulted in the arbitrary separation of the bottom organisms into macroscopic and microscopic faunas. Up to the present time, practically all the work has been concerned with the macroscopic forms. Only a few investigations of considerable duration and magnitude which are confined to the microscopic fauna alone are known to the speaker and results from them generally remain to be published.

The benthic fauna in general, in company with the rest of fresh-water forms, has been aptly characterized by Carpenter (1928) as "an immigration fauna." It is possible that the ancestors of some of the present-day insect members of this group may have sprung from swamp inhabiting forms of a long past age but it is commonly agreed that the aquatic adaptation of certain insects today has been secondarily acquired. This seems certainly true for the benthic forms. And what is true of the insects in this connection is quite as valid for the other groups. The bottom dwellers of our lakes today trace their ancestry either to terrestrial forms or to early invaders from the sea. Carpenter, although agreeing in general to the immigration theory mentioned before, suggests the interesting possibility of a fresh-water origin for the Protozoa and perhaps for life in general.

However that may be, it is obvious that any forms which might have invaded fresh waters from the land, secondarily or otherwise, would first have populated the littoral regions. No great experience with the bottom animals of our lakes is needed to convince any one of the clear relationship between the littoral and the sublittoral fauna. The picture is not quite so clear when one considers the question of the origin of the profundal benthic fauna. Without taking the time here to attempt a defense of the position the speaker confesses to the conviction that the true profundal benthic fauna is a *selection* fauna, recruited from the sublittoral and littoral zones and reduced today to a few hardy and highly

adaptable species through the medium of many purges at the hand of the seasonal cycles.

One of the problems, which from the early days of the present century has attracted students of this subject, has been that of the distribution of the animals over the lake floor. It was not so many years ago that evidence was first offered showing that the distribution was not uniform from shoreline to abyss, but that it was, instead, clearly marked by modes and peaks into zones. It has been amply demonstrated within the last 10 or 15 years that there is both a qualitative and a quantitative variation of the benthic fauna with depth.

The enormous diversity of lakes provides exceptions to almost any statement one may make about them but in general it is true that quantitatively the fauna increases with depth down to an optimum level somewhere within the lower littoral or upper sublittoral and then decreases with depth to a minimum within the deepest regions. Some of the exceptions referred to will be considered in a later paragraph. Qualitatively there is a somewhat similar situation, but the decrease within the profundal is tremendously accentuated in a qualitative sense. As has been stated before, only a few species persist into the lowest levels of the lake floor, but these few kinds may under certain circumstances provide enormous populations.

Probably the most striking characteristic of depth distribution of the benthic fauna is the *concentration zone*. When the speaker first proposed this term (Eggerton 1931) the following statement was made: "... there was a distinct zone in which the individuals of the benthic fauna were considerably more numerous than immediately above or below. This feature of the depth distribution, which repeatedly occurred at certain seasons of the year, will be referred to hereafter (in this paper) as the concentration zone." The data presented in several papers which had appeared previously actually show a well developed concentration zone to have been present in the waters investigated, but

little mention of the phenomenon seems to have been made before that date. Adamstone and Harkness (1923) and Adamstone (1924) reported on their studies of the bottom fauna in Lake Nipigon and their results plainly showed a concentration zone in that lake. Lundbeck's work (1926) demonstrated a sharply defined concentration zone in many of the northern German lakes. Rawson (1928, 1930) in excellent reports on the bottom fauna of Lake Simcoe described the same characteristic of depth distribution of the benthic fauna and like Lundbeck discussed the phenomenon in relation to environmental factors. Since that time the same type of depth distribution has been reported from many lakes in Europe, Asia, and North America. Recently, it has been shown (Eggleton 1936, 1937) that the distribution of the benthos on the floor of Lake Michigan exhibits the same feature. This investigation extended over a six-month period during each of two consecutive years and in "Each year a pronounced concentration zone was present between 35 and 50 meters with its peak close to the 42-meter level in both seasons." Miyadi, in his extensive series of bottom fauna studies on Japanese lakes, not only clearly demonstrated a concentration zone but also reported additional interesting observations which have contributed much to our growing understanding of the ecology of the benthos.

Introduction of Ekman's dredge, as has been intimated, marked a milestone in the development of benthic biology. Nevertheless, as it was first introduced a rather serious sampling error was inherent in the apparatus. The modification now known as the Ekman-Birge dredge largely corrected this situation and out of this fact there later developed an increasing interest in the vertical distribution of the benthic animals within the substratum. Many authors have discussed the matter and still more have offered data pertinent to the question but no exhaustive study of the problem has yet been made. Probably the best single contribution to this subject is that of Lenz (1931) who investigated this

vertical distribution by means of specially designed apparatus. In most lakes of northeastern United States which the speaker has had an opportunity to observe the macroscopic animals are almost wholly confined to the upper few centimeters of deposit. The depth to which they penetrate depends on several factors, but probably most of all on character of the deposit itself. Moore (unpublished) found several very interesting and surprising things in connection with the vertical distribution of the microscopic fauna within the profundal muds of Douglas Lake. Still further work is needed in this subject.

Conditions of existence within the bottom deposits are probably more stable than within the limnetic regions just above. And yet in the bottom sands and muds the environment is never quite at rest. Seasonal changes in the atmospheric climate produce profound effects in the ambient medium of the limnetic zone of our temperate and polar lakes and these changes in the superimposed water, in turn, strongly affect life in the bottom deposits. These changes are strikingly reflected in the seasonal variations of the fauna and again take the two forms, qualitative and quantitative. In typical eutrophic, temperate lakes of the second order, for instance, the qualitative composition of the benthic fauna will vary considerably with the seasons at any particular level and likewise in such a lake there are often enormous fluctuations in terms of the numerical abundance of the individuals of the constituent species. To cite but one example, the author found that the profundal benthic fauna of Third Sister Lake within the 18 meter contour varied qualitatively from a maximum of six or seven species in spring and fall to two or three in midsummer or midwinter stagnation and quantitatively from about 1,500 to more than 70,000 individuals per square meter. It should be pointed out in passing that one of the prime causes for this tremendous quantitative variation is the phenomenon of emergence in the life cycle of the predominant insect members of the fauna.

INTERRELATIONSHIPS OF THE BENTHIC
FAUNA

The benthic fauna constitutes one of the major links in the fundamental food chain of a lake. Although lakes vary greatly among themselves they also exhibit many characteristics in common with certain others. It is thus possible to place them in definite classes. Further, certain benthic organisms tend to be associated with certain kinds of lakes. Recognizing these facts, several limnologists, Europeans especially, have attempted to classify lakes on a basis of their typical or predominant benthic animals. Usually these have been profundal forms and we consequently read of "Corethra lakes," "Tanypus lakes," "plummosus lakes," "Tubifex-Pontoporeia lakes," and several others. The validity of these schemes, advanced by various Scandinavian, German, and Russian workers is probably sound for the north European lakes. Whether they, or some modification of them, will be found to fit American lakes remains to be seen. Little attempt has been made to apply these criteria to waters in the Western Hemisphere. Certain Japanese workers seem to have found the types applicable in some measure to the lakes of their islands.

Previously, in this paper, mention has been made of the intimate relation between type of substratum and type of fauna inhabiting it. There are several categories of important factors in the ecology of bottom animals, for example, general type of lake, major region of the lake floor, physico-chemical nature of the superimposed water, and the like, but within each of these major realms of environmental influence the type of bottom is in its own right a dominant factor. It is true of course that the mere presence of a flat rock outcrop within the profundal zone of a deep lake will not produce a faunal complex in any way similar to a flat rock fauna from the littoral of that or another lake. But a muddy bottom in a shallow bay of one eutrophic, temperate zone lake will tend to support a fauna very similar to that inhabiting a like situation in another lake of the same general type.

It is always necessary to remember in this connection that not only may some other condition supersede character of the substratum as a dominant factor, but that the reverse may also be true and type of bottom become the determining influence in otherwise similar habitats. We know all too little as yet concerning the exact effect of different kinds of bottoms and we lack well standardized and distinctive criteria for judging and recording the exact nature of the bottom materials. A moment's reflection will call to anyone's mind the wide diversity in the intrinsic nature of such a substance as sand, or flat rock, or mud. From what we know now it seems probable that from the standpoint of selective action on the fauna the major types of substratum may be listed as flat rock, boulders, rock and gravel, gravel, sand, clay, and what for want of more discriminatory terms we are compelled to lump into one great heterogeneous class and call simply mud.

Many students of the subject, the author included, have written of the pronounced effect of the physico-chemical factors of the superimposed water upon the life and activities of the benthic animals. All these influences fall into two major classes: those which are inherent in the nature of water itself and those others which act through the water as a medium. In the first category are such characteristics of water as weight, which results in pressure, relative incompressibility, density, low viscosity, transparency, buoyancy, and others. Within the second class will fall such factors as temperature, light, current; dissolved substances, gaseous, solid, organic and inorganic; turbidity, color and the like.

Each calendar year is divided, for the inhabitants of a lake, into *four limnological seasons*: spring turn-over, summer stratification, autumn turn-over, and winter stagnation. The annual cycle of this chain of events profoundly affects the organisms which live in and on the bottom. This is especially true, of course, in the second order lakes within the higher latitudes of the temperate zone and the lower ones of the polar zone. Likewise it is of extreme

significance in the ecology of the profundal organisms, although the alternate freezing and thawing, together with the succession of the quiet of winter and the storms of fall and spring; the cold and darkness of winter and the warmth and light of summer certainly are calculated to relieve any tedium in life of littoral forms.

It has been shown repeatedly that benthic organisms, like all others, have rather definite optimal ranges for each physico-chemical factor. Probably Liebig's famous "Law of the Minimum" becomes quite as effective sometimes in the life of benthic animals as it ever is in the life of the plants for whose special benefit it was first promulgated. Studying the profundal bottom animals experimentally both in the lake and in the laboratory the speaker has found them to be susceptible to variations in the physico-chemical factors imposed by the ambient medium in varying degree. Perhaps two of the most interesting results of these studies have been that (1) it is possible to produce conditions resembling those which obtain on the profundal lake floor during prolonged stagnation which are so severe that all the organisms are killed and sometimes possible to find similar conditions with similar results in nature, and (2) certain lakes vary so far in this direction even to becoming permanently stagnant in their profundal zone and hypolimnion that the result is the production of a veritable biological desert. In this connection certain facts always stand out clearly, namely, no factor in nature ever acts alone, every one always is acting in the presence of all the others; and usually the effectiveness of variations in one factor is greatly increased when operative in the presence of variations in another. A small decrease in dissolved oxygen will, for instance, often be more deleterious in the presence of a high temperature than a greater decrease in oxygen would be if unaccompanied by any such temperature variation.

Biotic interrelations of the bottom fauna are incompletely known. And much that has been discovered is, for obvious reasons, related to the importance of this association

as a source of fish food. The interspecific and intraspecific relations within the bottom fauna itself remain largely to be disclosed. Parasitologists have been exceedingly busy during the last few decades and have added very significantly to this phase of benthic biology, although here again it has most often been the parasitic embarrassment of some fish or other vertebrate host, such as man, which has been the real motivation, rather than any altruistic and purely disinterested scientific curiosity concerning the biology of benthic invertebrates which has resulted in our enlightenment.

Among the many purely biotic interrelationships, about which we know so little, a few phenomena have been given some attention. One of these which may be a potent cause in population fluctuations is migration. In some species the individuals actually change their location on the lake floor to a significant extent, in others the death of many individuals within one stratum and the birth (or hatching) from vast numbers of eggs in other and perhaps successively adjacent zones, or the pupation and emergence of insect members of the fauna, may give the semblance of significant individual migration when actually particular specimens may have moved little if at all. Such phenomena probably combine to cause the shift of the concentration zone up and down the lake floor which occurs in some, perhaps many, of our lakes of this region. The speaker is convinced that insect life cycles, including pupation and emergence, and their relations to and effects upon benthic productivity are inadequately understood and offer a fruitful field of work for some one.

Food, feeding, predators and enemies, symbiosis, commensalism, and host-parasite relationships all play important roles in relation of the benthic fauna, both within its own ranks and in the larger realm of the life of the lake as a whole. Members of the benthos serve both as food for and as feeders on other groups within the lake. Many of them also stand in the important relationship of detritus feeders and coprophagous scavengers, thus serving as an indis-

pensable link in the cycle of the fundamental food supply of the microcosm which is their home.

BENTHIC PRODUCTIVITY

Biological productivity has been stated by at least one author (Welch 1935) to be "the central influence" of limnology. No one, I am sure, will deny its key position in the complex of lacustrine biology. Various criteria of productivity may be selected with equal justice. Quite commonly it is assumed that it is to be measured in terms of fish production. That is one satisfactory equivalent. It is quite possible, however, and often useful to think of biological productivity in terms of the benthic fauna. When so considered the two measures most commonly employed for expression of productivity, namely *standing crop* and *annual production* may be expressed in terms of kilograms per hectare of dry organic weight; as crude protein, or available nitrogen; or as number of individuals per unit area. Whatever the unit or mode of measurement it will be found that, as in so many other ways, lakes vary enormously in benthic productivity just as farm land does for wheat or corn. The intricate interplay of all the physical, chemical, and biological factors which combine to influence or control benthic productivity provides today, and will provide for many years to come, one of the most interesting and most challenging phases of benthic research.

The contribution of the benthos to the productivity of the lake as a whole is large indeed, regardless of the criteria selected. Entirely aside from the strategic position occupied by these bottom feeding animals as consumers of otherwise useless and lost food and therefore as important contributors to the maintenance of the cycle which must not run down if productivity is to be kept up, they occupy in their own right a place of significance in the production of the total organic substance present in or produced by the whole lake. One need only mention the tremendous figures of more than 33,000 individuals per square meter found by Juday within the profundal of

Lake Mendota, or the 71,000, and more, individual macroscopic organisms per square meter in the muddy floor of Third Sister Lake, or the more than 20 kg per hectare of dry organic weight on the floor of Lake Michigan to show that the benthos does contribute significantly to total lake productivity.

FUTURE NEEDS IN BENTHIC STUDIES

Scattered throughout the foregoing pages there have been frequent suggestions of problems needing further investigation and offering challenging fields of research. However, several points need yet to be stressed in this connection. There are many unanswered questions awaiting a fertile mind and ambitious hand. Why, for instance, has no one succeeded, unqualifiedly, in the attempt to rear fresh-water sponges in captivity? How do the profundal benthic animals derive their oxygen for metabolism in an anaerobic environment? Which if any of the several suggestions offered to explain the diurnal migration of *Corethra* larvae is the correct one? Does the haemoglobin of *Chironomus* larvae really serve the organism significantly in a stagnant lake bottom? One might continue such questions indefinitely, but the few here proposed will illustrate the point.

Several major phases of lacustrine benthic faunal research are wide open fields. The task during the past summer of writing a symposium paper on fresh-water communities (Eggerton 1939) brought forcibly to the speaker's mind the great dearth of benthic studies made from the standpoint of bottom animals as members of animal communities. Few if any complete life histories have been worked out for the species of the benthos. There is still much need for many more long-term qualitative and quantitative investigations. Much of our classification of lake types, biotic forms, environmental regions, habitat groupings, and the like will have to be revised when we have more extensive and adequate knowledge on a wide variety of questions. As has been previously suggested study of the microscopic benthic fauna is practically a virgin territory. Our knowledge of the

bottom fauna of our five Great Lakes is woefully inadequate and incomplete. Finally a phase of benthic study which has been hinted at before in this paper and which needs many able students may be characterized by the term "experimental." There, perhaps, is the most promising and provocative aspect of the whole subject.

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THE POSITION OF FISH AND OTHER HIGHER ANIMALS IN THE ECONOMY OF LAKES

By F. E. J. FRY

ONTARIO FISHERIES RESEARCH LABORATORY, DEPARTMENT OF BIOLOGY,
UNIVERSITY OF TORONTO, TORONTO, ONT., CANADA

ALL vertebrates which are not strictly marine contribute to the economy of lakes. However, there are great differences in the intimacy of their relations with the lacustrine environment. Many are related to conditions in the water only through their presence in the drainage areas. Others, while completely dependent on air for breathing, may obtain their food from lakes. To this group belong the aquatic mammals and birds. The aquatic reptiles and amphibians are more closely associated with the water than are the other air breathing vertebrates, since they can utilize the dissolved oxygen in the water with varying degrees of efficiency. The group of vertebrates most completely related to the economy of lakes is the fish. In our latitudes fish are confined to the water all their lives, except possibly for a short nocturnal excursion through the grass which eels may undertake. Because of their complete dependence on the aquatic environment, the relations of the fishes will be discussed at greatest length here, in spite of the fact that man, a mammal whose feet are not even webbed, is the species which has the most profound effect on the economy of lakes, and might from that point of view claim the major portion of our attention.

Since the fishes depend for their very existence upon conditions in the water, it might be more appropriate, if the title of this paper were to refer to fishes only, to speak of the position of lakes in the economy of fishes rather than of the position of fishes in the economy of lakes, for the lake is the independent variable in the relation. The fish has to conform to the extent of being physiologically compatible with the conditions of existence in a given body of water, and then within this limited sphere it may contribute its share to the economy of lakes.

The relation between fishes and their aquatic environment is a very intimate one. Fish possess no hair to insulate their body from the ambient temperature. There is no vestibule between the environment and the respiratory surfaces comparable to the lung of the air breather. It falls to the lot of the fish to avoid what unfavorable conditions it can by migration, and to endure to the limits of its adjustment those which it cannot avoid. Thus in certain lakes, conditions are impossible for the existence of a given species of fish. In other lakes the species exists under more or less unfavorable circumstances. In still others the physical and chemical environment may be so completely favorable as to allow the same species full scope for its development, provided its members can obtain sufficient food.

Since the development of an animal depends on nutrition, as well as upon favorable physical and chemical conditions in its surroundings, the presence of a suitable supply of food is also essential. The food organisms are in their turn limited in their own existence to a range of physical and chemical conditions which they can tolerate, or by the necessity for a suitable supply of food, either in the form of other organisms, organic matter, or more primary chemicals. As well as conditions in the immediate environment and the nature of the food supply, factors which affect each individual, there is the factor of predation which affects the welfare of the species as a whole.

It is by compromise, by surviving under a wide range of physical and chemical conditions, and by being able to live with and upon a wide range of associates, that fishes contribute as much as they do to the economy of lakes. Fishes can go far in this compromise. Twenty pound lake trout can turn to *Daphnia* when no other food comes

within their range. Unfavorable conditions can be avoided by vertical migrations which take the members of a species into strata where life is possible for them. When migration is impossible or of no avail, seasons when complete activity cannot be maintained may be spent in quiescence or in fasting.

In this paper the interaction of the inanimate environment and the animate community of lakes on the welfare of the fishes to be found in them, is illustrated by a short discussion of some effects of temperature on the feeding of fish. The relation of these effects on feeding activity to the problem of production of fish are considered. In conclusion the methods of attack on this problem that appear to have been most successful are mentioned and the part each may possibly play in the future are tentatively assessed.

Fish occupy various places in the food cycle which are often more than once removed from the primary plant food. In general each species has certain morphological characters which are related to the nature of its food, thus fish living to a large extent on bottom food possess inferior mouths; species living on plankton, slender and more numerous gillrakers; species living on other fish, large mouths and sharp teeth; but these relationships are not rigid. Anglers casting a fly for trout occasionally find that their efforts are rewarded by the rising of a sucker. The cisco, although it has gillrakers which would class it as a typical plankton feeder, by no means confines its diet to the micro-crustacea. The lake trout, whose large mouth and sharp teeth are typical of an actively predaceous fish, in some lakes feeds almost exclusively on the larger plankton, crustacea and other small aquatic invertebrates such as *Corethra*.

On the other hand fish are by no means indifferent to attributes of their food other than its size. Certain species, and indeed certain individuals, may show a marked preference for a particular food organism, although other organisms may be equally or more easily available. Pearse and Achtenberg (1920) record the specific preferences

of six different species of fish in Lake Wingra. Plankton feeders do not always remove their food from the water by random straining (Battle *et al.* 1936; Wagler 1937; Langford 1938). Ricker (1937) relates that when a number of fish of the same species, *Oncorhynchus nerka*, were confined in a small space, certain individuals selected *Cyclops* from the plankton present in contrast to the *Daphnia* which was more favored by their fellow prisoners. Thus while there may be considerable latitude in their choice, fish select preferred foods from those offered within their range.

To be utilized, food must not only be of suitable size and quality but it must also be available. This may not be the case even when the fish and the food organisms are present in the same lake. Langford (1938) shows that during August, the cisco in Lake Nipissing feeds on *Mysis* to a much greater extent during the day than it does at night. Since *Mysis* migrates upward at night while the cisco does not, this diurnal variation of the presence of *Mysis* in stomachs is quite understandable. A second illustration of the effect of spatial separation of food and feeder is offered by the seasonal and annual variation of the amount of perch in the stomachs of lake trout from Lake Opeongo, which is shown in Fig. 1. The number of perch eaten by the lake trout in Opeongo in early summer is largely dependent upon the sharpness of the thermocline. In June of 1937, the amount of perch in the stomachs of Opeongo trout was negligible, while in 1938 they were the most important article in the diet. Langford and Martin (unpublished) have shown that perch are distributed downward to strata having a temperature of about 15° C in that lake, and it is probable that lake trout and perch overlap in their distribution over the temperature range of at least 14–17° C in summer. During June this temperature range covered a far greater depth of water in 1938 than it did in 1937. In late July and August the difference in sharpness of stratification is not so marked.

While most species of fish do not make such extensive vertical migrations in search

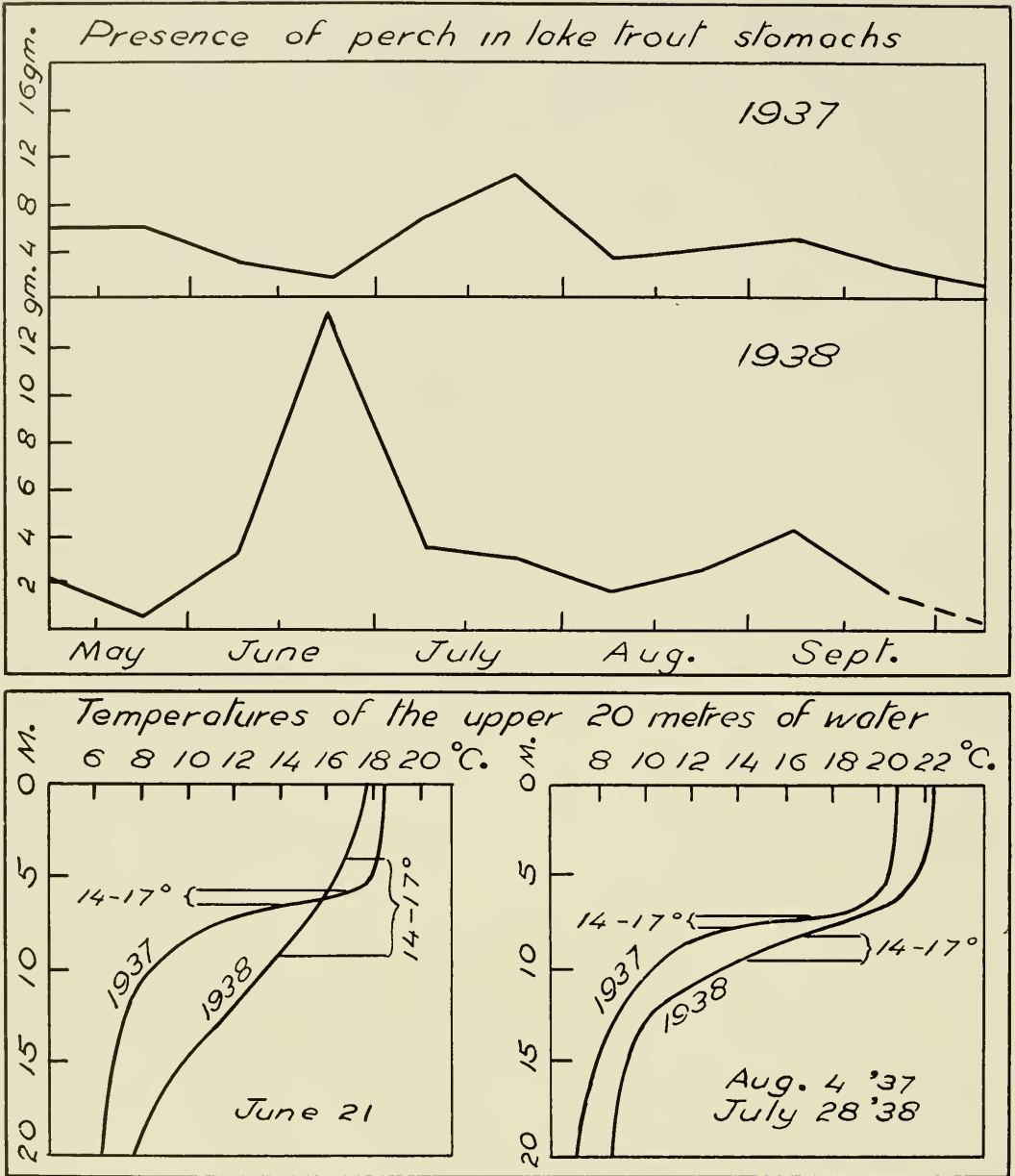


FIG. 1. Amounts of perch found in lake trout stomachs in 1937 and 1938, Lake Opeongo, Algonquin Park, Ontario. The absolute values in the two years are not directly comparable. The weights given for 1937 are calculated from the lengths of the perch ingested, whereas the weights for 1938 are the actual weights of the stomach contents. The calculated weights are at least twice the actual weight of perch present in the stomachs, and the graph has been adjusted by plotting the values for 1937 on half the scale used to plot the values for 1938.

of food as take them through barriers set up by thermal stratification, there are some exceptions. Pearse and Achtenberg (1920) found that perch invade the stagnant hypo-

limnion of Lake Mendota to feed, although they would soon die if they remained there. Similarly Juday and Wagner (1908) found that lake trout commonly entered waters in

which the oxygen was too low to support them for any length of time. A number of fish make nocturnal excursions into shallower water and feed there.

Further, even though food and feeder may be present in the same stratum there may be physiological causes which affect the utilization of food. The general effect of temperature on metabolic rates and the familiar annual cycle of growth are too well known to require discussion here, but must always be taken into consideration. Fish do not feed over the whole range of temperature within which they can survive. Pearse and Achtenberg (1920) state that the perch in Lake Wingra take very little food during the warmest period of the summer. Mackenzie (1934) and Blair (1938) found that there were upper temperature limits for the cod and the salmon beyond which feeding decreased markedly. When feeding has once been inhibited by too high a temperature the fish may not start to take food again immediately upon entering more favorable temperature conditions. In an experiment performed with salmon parr (Fry and Kennedy unpublished) the water in which they were living was warmed gradually from 18° C to 28° C over a period of 20 days. At 28° C the parr stopped feeding, and, although the water temperature was quickly reduced to 10° C and maintained at that low temperature, the fish did not feed again until 15 days later. The feeding behavior of the Lake Nipissing ciscoes (Fry 1937) is probably an instance of such an effect. In Lake Nipissing, ciscoes remain in the epilimnion until their upper feeding temperature is passed. On ceasing to feed they migrate down into the hypolimnion where they remain until early autumn. Throughout their stay in the hypolimnion a large proportion of them do not feed at all. Further, the group which does feed is not a chance section of the population but is made up of individuals which migrated early; these are for the most part the larger and older members of the population. Angling statistics for both the lake trout (Fry and Kennedy 1937) and the rainbow trout (Mottley 1937) give

evidence that these fish behave similarly to the cisco in respect to their summer feeding activity.

From a consideration of circumstances which affect the utilization of food, such as the examples given above, it will be realized that variations in growth are influenced now by one factor and now by another. In a discussion of the growth of ciscoes in certain Wisconsin lakes, Hile (1936) states that there is a direct correlation between growth in weight and the length of the growing season, but there is no relation between abundance of food and the rate of growth of ciscoes. He makes the following statement, “. . . it is quite probable that the cisco does not thrive in the physical and chemical conditions most conducive to a large population of food organisms . . .” Thus as Langford (1938) points out, poor growth may result on the one hand from sparse food, and on the other from unfavorable physical and chemical conditions.

Differences in feeding are often strikingly reflected in fish populations by dwarfing, although all dwarfing is not to be interpreted as being due merely to lack of food. Certain types of dwarfing are physiological, since dwarf and normal races often occur in the same lake. Examples of this kind are to be found in the smelt (Kendall 1927), the common sucker (Dence 1927), and the northern sucker. Other cases of dwarfing are more closely dependent on feeding conditions. Sometimes too high a density of the feeding population results in a diminished food supply for each individual. Sometimes food suitable to allow rapid growth is absent from a given lake, or if present is spatially separated from the feeder during the growing season. Finally, as has been pointed out the fish may not feed because of adverse physical and chemical conditions, even though food is present. Whatever the cause, dwarfing is usually associated with a high population density.

Poor growth, of which dwarfing is the extreme, need not be looked upon as an unmixed evil, even from a strictly economic point of view, for it appears to be responsible to some degree for the maintenance

of populations of certain species of fish in small bodies of water. The lake trout is one of these species. In Ontario and probably elsewhere small lakes of about 30 acres which contain lake trout usually harbor a small race of the species with a high population density. Occasionally such a lake will be found to contain large trout but then the density will be extremely low. It is easy to believe that in such lakes the total number of trout may fall to so low a figure that some accident could wipe out the race. Thus there may be a selection mechanism at work which prevents the maintenance of lake trout in small lakes in which conditions favor their growth, unless some influx of lake trout from neighboring waters could reseed the lake after such an accident.

Because of the complexity of the relationship which exists between food and feeder, the relation between production of fish and what may be termed "basic productivity" is equally complex. With all other conditions favorable, a limit to the production of fish would finally be set by the "basic productivity." In practice, however, this limit may not be even closely approached. Even in the ocean where conditions are more uniform, the communities have not evolved to a point where food is always fully utilized. The fluctuations in the size of year classes, and the effect of these fluctuations on the density of the standing population, prove that food is not always the limiting factor. Dominant year classes also occur in fresh water (Hart 1932, Tester 1932, Hile 1936). Although the phenomenon of dominant year classes is evidence against the belief that food always controls the production of fish, in times of maximum abundance it may become the limiting factor. This is well shown by the work of Foerster (Ricker 1937) on the sockeye salmon in Cultus Lake. Foerster found that when the number of seaward migrants was 1.5 millions or more, the size of the individuals was considerably below that attained in years for which the number of migrants was a million or less. Ricker (1937) calculates from Foerster's data that the density of sockeye fingerlings in Cultus Lake in 1932 was great enough

to bring about an appreciable reduction in the entomostracan food supply.

The variation in average size and population density which is found in lake trout populations shows the complexity of the relations between various factors of growth, reproduction and predation. The average size of lake trout taken by anglers in a number of Algonquin Park lakes and the relative abundance of these fish as expressed by the number of fish captured per 100 boat hours of fishing effort, are plotted in Fig. 2. There are wide variations in the ease with which lake trout can be captured which are related to the size of the fish that are taken, but the relationship is not a simple proportionality. Lakes in Algonquin Park in which all the lake trout are 13 inches or less in length offer practically no fishing at all. Lakes in which the average length of the trout captured lies between 14 and 18 inches may contain either an abundance of fish of catchable size or practically none. Lakes in which the average length is greater than 18 inches contain moderate numbers of larger fish; the number taken per unit effort being inversely proportional to the average length of the fish captured.

This relationship is apparently the outcome of the interaction of at least three factors: (1) the effect of predation by man, (2) variations in the size at which lake trout reach maturity, and (3) the influence of the presence of large trout upon the density of their own populations. It is only the second of these factors which is directly related to food and feeding. Since the tackle used in fishing for lake trout is not efficient for taking them smaller than about 14 inches, trout smaller than that do not enter into the production as far as man is concerned, although there may be large numbers of them present. Among the populations of lake trout in different lakes in Algonquin Park there are some in which the females are only 13 or 14 inches long when they reach maturity, others in which the females are 18 inches long before maturity, and others which lie between these extremes. Thus populations producing fish with an average length between 14 and 18 inches

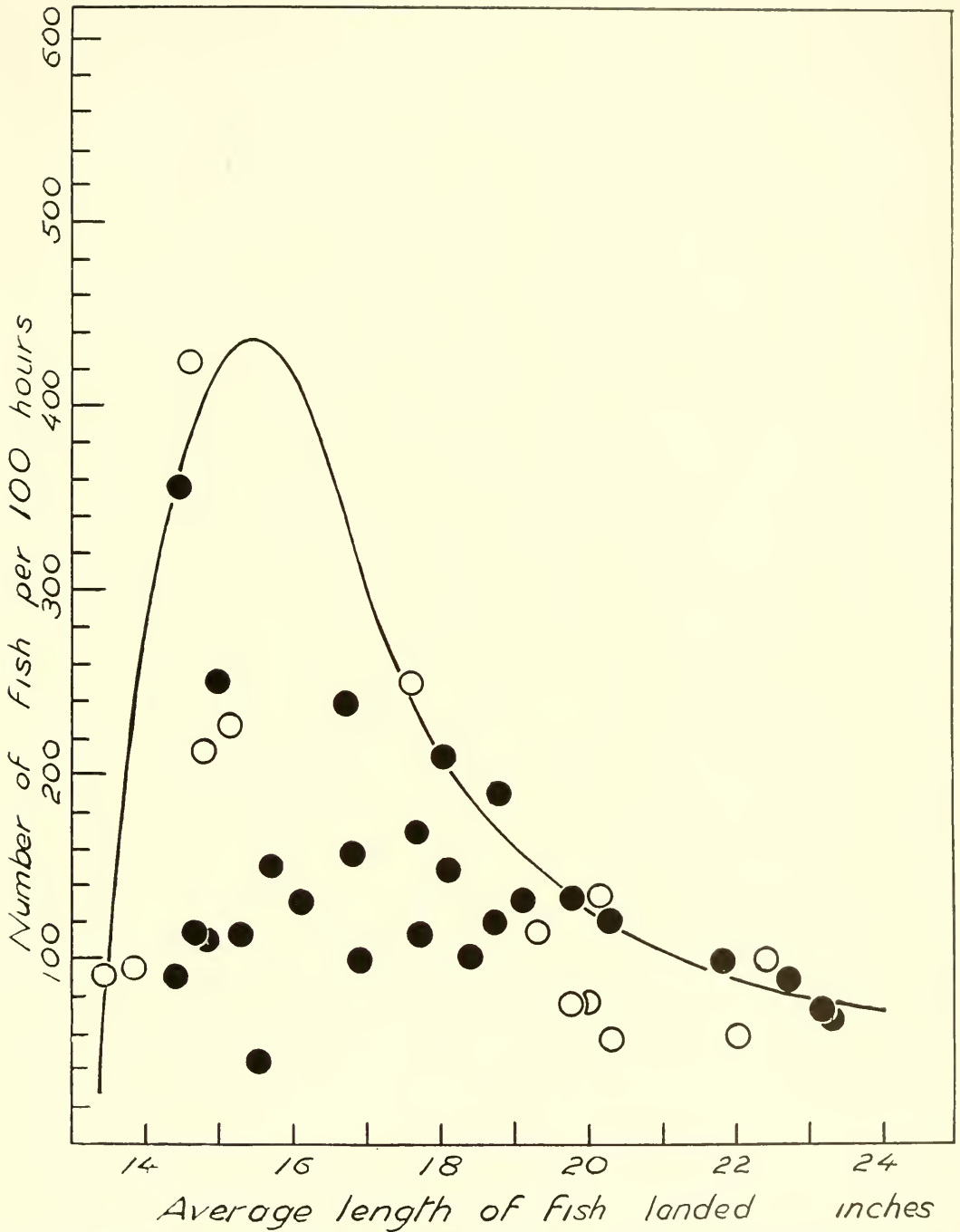


FIG. 2. Relation between average length of lake trout captured in certain Algonquin Park, Ontario, lakes and their availability as expressed by the number of fish captured per 100 boat-hours.

are made up either of individuals capable of abundant reproduction, or perhaps not capable of any at all. Hence in the former case they may be maintained at a relatively high density, or in the latter they will in extreme cases practically disappear. Lake

trout over 19 inches long are mature in all Algonquin Park lakes, and above this size reproduction is no longer a limiting factor. Populations from which the fish captured average 20 inches or more are characterized by a progressive scarcity of the smaller size classes, apparently due to the predatory activities of the larger trout. In these lakes production is limited by the presence of large trout, and the number of fish taken per unit effort can be increased by the removal of these by fishing. It will be realized, of course, that Fig. 2 shows only the standing crop, the annual production being influenced by the average age of the population as well as by its average density.

Owing not only to the complexity of the factors involved, but also to the fact that quite different causal agents can produce the same effect, it would seem that there is no hope of devising a workable index with which to classify lakes according to their usefulness in producing fish desirable to man. Since there is no prospect of progress along such a royal road, it would appear that advance toward the solution of our problems of productivity lies along paths which we are already taking. Judging from the history of limnology, the most profitable attack on problems of fisheries production lies in the following steps: (1) measure production, (2) study the organism in nature in detail, and (3) supplement the field observations with laboratory experiments.

Measurement of production is done by the collection of statistics of capture of the animals sought in commerce and in sport. The collection of commercial records is now taken as a matter of course and the collection of statistics of sporting fisheries is becoming increasingly more widespread. Also it is realized that something more than records of total capture are necessary, and information is being commonly collected concerning fishing effort and size composition of the catch. There is a growing tendency to formulate theories which, while taking into account all the biological information available, are nevertheless primarily founded upon empirical relations observed

between the abundance of the population and the history of the removal of its members by man. Of these probably the most outstanding achievement to date is that evolved and put into practice by the International Halibut Commission (Thompson 1935).

Experiments are essential both to supplement observations in the field and to test practices proposed for the improvement of production before they are introduced into management on a large scale. It is often impossible to predict with certainty the outcome of steps which might at first glance appear to be certain to lead to improvement. If the lake trout may be referred to again for an example it might be pointed out that measures taken to improve the growth of a slow growing population of this species need not necessarily improve the production of fish, but may conceivably lead to a poorer fishery than before. With the methods of angling that are currently in vogue, lake trout shorter than 12 inches are rarely captured and thus there is a minimum size at which lake trout take the hook which acts as surely for their conservation as does a legal length in other species. In lakes where lake trout mature at a small size their own habits protect them from capture until the season in which they become mature. If the rate of growth increased, such a population would lose this natural protection in large measure, because with more rapid growth the fish would be larger at maturity, and would be liable to capture a year or even two years before the season in which they spawned. Hence if the population were subjected to a high fishing intensity any initial improvement of production resulting from improvement in growth would soon be more than lost because of the greater effect of predation upon reproduction.

Experiments which are designed to analyze the factors underlying the behavior of the organism observed in nature are of more fundamental importance than those designed to test theories before they are put into general practice. Shelford (1934) has pointed out the importance of being thor-

oughly familiar with conditions in the field before drawing conclusions from laboratory experiments. It must also be recognized that laboratory experiments give physiological answers rather than ecological ones. This is both a pitfall and an advantage. Too often the attention of the experimenter is focussed upon an effort to duplicate in the laboratory physical and chemical conditions which may be found in the field, and he does not take thought to consider fully just in what way these conditions are acting upon his experimental animals. There have been experiments by which the relative sensitivity of species towards unfavorable conditions have been measured

Thus, although it is desirable to get a general index of resistance, the rate of dying in a lethal concentration of dissolved gases is dependent upon a very complex interaction of factors and Wells' scale of sensitivity, while holding true for the conditions of the experiments, cannot be trusted to predict the reactions of those species to sublethal concentrations of the gases in question, nor even to be a measure of the order of concentrations of gases which are the lethal thresholds of each species.

Other measures of sensitivity towards carbon dioxide have been made which give a scale differing from that of Wells. If fish are sealed in bottles containing water

TABLE 1

COMPARISON OF THE RELATIVE RESISTANCE OF VARIOUS SPECIES AS MEASURED BY WELLS (1918) AND THE ORDER OF SENSITIVITY TOWARDS CARBON DIOXIDE AS MEASURED BY POWERS *et al.* (1938) AND BY FRY AND BLACK (1938).

Order of resistance (Wells)		Order of Sensitivity (Powers <i>et al.</i> , Fry and Black)	
<i>Catostomus commersonnii</i>	} Lake Michigan	<i>Perca flavescens</i>	{ L. Erie
<i>Semotilus atromaculatus</i>	} N. Ill.		{ Alg. Pk.
	"	<i>Catostomus commersonnii</i>	Alg. Pk.
(<i>Chrosomus erythrogaster</i>)	"	<i>Micropterus dolomieu</i>	{ L. Erie
	"		{ Alg. Pk.
<i>Micropterus dolomieu</i>	"	{ <i>Ambloplites rupestris</i>	{ L. Erie
<i>Hyborhynchus notatus</i>	"	{ <i>Notropis cornutus</i>	Alg. Pk. }
<i>Notropis cornutus</i>	"	<i>Hyborhynchus notatus</i>	Alg. Pk.
<i>Ambloplites rupestris</i>	"	(<i>Chrosomus cos</i>)	{ Toronto
	"		{ Alg. Pk.
<i>Perca flavescens</i>	"	<i>Semotilus atromaculatus</i>	Alg. Pk.
<i>Ameiurus melas</i>	"	<i>Ameiurus nebulosus</i>	Alg. Pk.

by comparing the rates of dying of individuals in conditions which were lethal to the hardest. The experiments of Wells (1918) from which a scale of hardness of certain species of fishes was derived, were of this type. Because of the importance of this scale of hardness, it may be proper to insert here some criticism of the interpretation of the experiments on which it is based. When a fish is placed in a concentration of dissolved gases in which it dies rapidly, the rate of death depends on the ratio of surface to volume, on the rate of circulation of the blood, on the rate of gaseous exchange at the gills, on the rate of utilization of oxygen by the tissues, and on the ability of the animal to endure anoxia.

high in oxygen and charged with various concentrations of carbon dioxide, and allowed to die there of asphyxiation, it will be found that the amount of dissolved oxygen remaining in the water will vary according to the species and to the amount of carbon dioxide present. Such experiments have been carried out by Powers *et al.* (1938) and by Fry and Black (1938). Data from a number of such experiments are plotted in Fig. 3. The order of resistance of certain species in Wells' scale of sensitivity are compared with the order of the same species as measured by Powers *et al.* and by Fry and Black in Table 1. This comparison must be considered only as tentative, since there is considerable subspe-

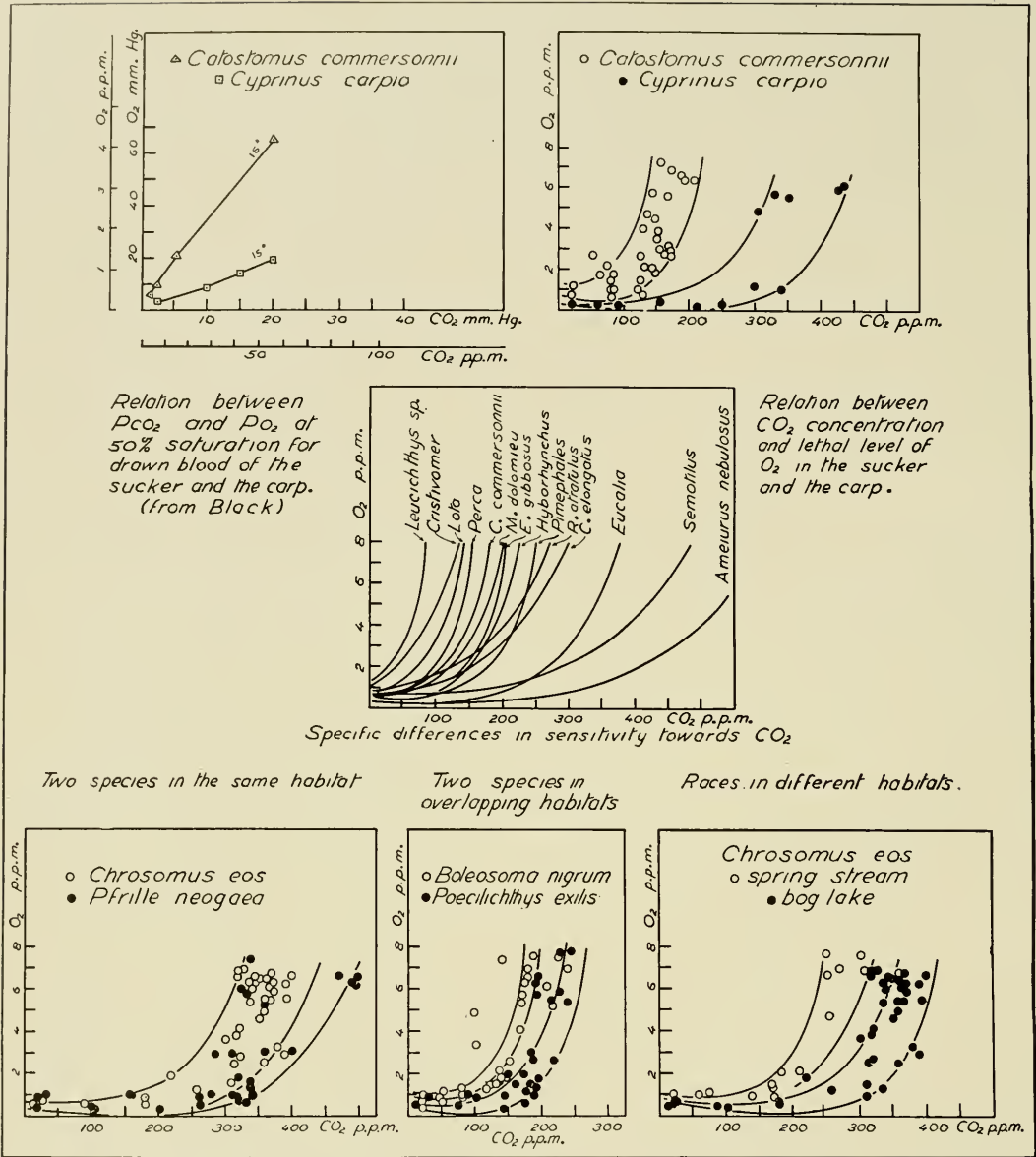


FIG. 3. Specific differences in the ability of fish to take up oxygen in the presence of carbon dioxide (from Black 1938 and Fry and Black 1938.)

cific variation in sensitivity but the order of the species is completely different. The concentrations of carbon dioxide used by Powers, and by Fry and Black lie almost completely out of the ecological range, yet the species measured, which include among them nearly all those living in Lake Opeongo, Algonquin Park, show a sensitivity which is directly correlated with

their vertical distribution in lakes in summer. Species most sensitive to carbon dioxide are found in the hypolimnion, species least sensitive are found in the weedy shallows. This correlation cannot be due to a causal relation between the stratification of dissolved gases and the sensitivity of the fish towards them for the gradients of carbon dioxide and oxygen are the reverse of

what would be expected to account for such a correlation. However, if the experiments are considered as throwing light on a physiological mechanism, they have much more meaning.

It is well known that carbon dioxide has a marked effect on the transport of oxygen by the blood of mammals. In the presence of relatively low concentrations of carbon dioxide their blood can become saturated with oxygen at relatively low tensions of that gas. On the other hand if the carbon dioxide tension is increased the blood cannot take up or hold oxygen to nearly the same extent. Accordingly the moderate tension of carbon dioxide in the alveoli and the higher tension in the tissues facilitate the shift of oxygen from the lungs to the blood and from the blood to the tissues. This effect of carbon dioxide on the ability of blood to take up oxygen is known as the "Bohr effect." Carbon dioxide has a similar effect on the blood of fishes, as has been shown by many workers. Particularly since the discovery of the biological anticoagulant heparin, it has been shown that the magnitude of the Bohr effect in fish blood differs greatly from one fish to another. It is often much greater than that displayed by the blood of mammals or there may be hardly any effect at all as Black (personal communication) has found to be the case in the catfish.

Blood curves for two fresh-water fish, the sucker and the carp, from Black (1938), are given in the upper left panel of Fig. 3 which shows the oxygen tension necessary to half saturate the blood in the presence of a given tension of carbon dioxide. These two blood curves occupy about the center of the range of sensitivity which has been found in fishes, and by way of a landmark it might be pointed out that a similar curve for man lies very closely to that of the carp.

When the curves for the levels to which oxygen can be removed in the presence of different concentrations of carbon dioxide by these two species, shown in the upper right panel of Fig. 3, are compared with the curves for the drawn blood, it will be apparent that the sensitivity toward carbon

dioxide displayed by the fish may be dependent upon the magnitude of the Bohr effect shown by their bloods. This is what would be expected on *a priori* grounds, for fish with blood very sensitive to carbon dioxide would be less able to take up oxygen in the presence of increasing carbon dioxide than would fish with blood that was more indifferent to the presence of that gas. Thus, and there is further evidence to support this view, the measure of sensitivity towards carbon dioxide as shown in Fig. 3 is in all likelihood a measure of difference in the Bohr effect displayed by the bloods of different species. Consequently it seems reasonable to infer that the correlation observed between sensitivity and vertical distribution of these species in summer is due to differences in the oxygen transport capacity of the blood.

With this brief mention of the part experiment plays in limnology our consideration of the position of fish and other higher animals in the economy of lakes is finished. No attempt has been made to review the subject exhaustively or to give more than a few references to works which are easily accessible in America. It may be felt that vertebrates other than fish have been shamelessly neglected throughout this discussion. It must be confessed that they have, but in justification it can be pointed out that the principles which have been mentioned here apply to other forms of life as well as fish. Again it may be felt that applied limnology has been overstressed. In defense it may be maintained that the only valid classification of limnology is into the practical and the not practical rather than into pure and applied. The differences between pure and applied science lie not in the subject matter but in the attitude taken towards it.

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